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This paper was prepared
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ABSTRACT

Peatlands are nutrient-limited ecosystems. Human activities are causing an increase in nitrogen (N) deposition, which may lead to fertilization of bogs and alter vascular plant densities and biomass. N deposition affects ecosystem function, and potentially alters the system's ability to sequester carbon. In the summer of 2005 we measured this effect in an ombrotrophic bog, Mer Bleue, near Ottawa, Canada with a fertilization experiment established in 2000.

We measured leaf-level CO_2 exchange with a LI-6400 portable photosynthesis system. We used these data to calculate the maximum rate of photosynthetic capacity (V_{max}) between the high fertilization (20NPK, 20 times the ambient summer N deposition, or 6.4 g N m^{-2} as NH_4NO_3, and 6.3 g P m^{-2}, 5.0 g K m^{-2} as KH_2PO_4) treatment plots and control plots. We quantified above ground vascular plant biomass through non-destructive measurements of stem height and stem number within the 0.6 x 0.6m quadrat where we measured net ecosystem CO_2 exchange. We destructively measured shrub biomass, number of leaves, leaf size, number of stems, C: N ratio of the leaves, and stem length for clipped plant samples collected from outside the CO_2 measurement quadrats. We also measured leaf area index, the mass of litter and litter cover with in the 0.6x 0.6m quadrats.

After five years of nutrient addition, above ground biomass of shrubs significantly increased between the control and high fertilization plots (20NPK). This pattern is perhaps explained by the increase in both stem length and leaf area with the fertilizer addition. A decrease in C: N ratio suggests that plants in the fertilizer treatments are taking up the added nutrients. However, an important difference was found in the leaf level photosynthesis data, which showed a significant decrease in V_{max} between the control and the high fertilization treatment. These results have important implications for the ecosystem response to environmental changes. The increase in biomass and litter production of vascular plants will have effects on carbon storage as a result of the decomposability of this matter. The increase in biomass may be offset by decreases in leaf-level photosynthesis, potentially altering the carbon uptake within the system.

Plant Response to Fertilization at a Cool Temperate Peatland

By

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INTRODUCTION

Wetlands:

Wetlands are some of the most important ecosystems on the earth. They are ancient systems valued for the functioning of their hydrological and biogeochemical cycles. Wetlands provide unique habitats with rich biodiversity. There are various types of wetlands systems, varying from mangrove swamps to boreal peatlands. Wetland systems are found on every continent except for Antarctica. Wetlands exist within a diverse range of climates and can be found in cold climates such as, Alaska to warmer climates, such as Sudan (Mitsch et al 1993). These ecosystems are found in many places across the globe, however they only account for approximately 4- 6 percent of the world's ice free land surface, or 8.6 million km^2 (Matthews and Fung, 1987, Mitsch et al. 1993, Keddy, 2003, Ramsar, 2005). Of the total wetland area approximately 3.8 million km^2 of it is boreal peatlands; 3.5 million km^2 of boreal peatland area is located primarily in Russia, Canada, the USA, and Finland and Scandinavia (Gorham 1991). Canada contains an area of 127.2 million hectares of wetlands, which is equivalent to approximately 14 percent of the country (Zoltai et al. 1988 and Mitsch et al. 1993).

What is a Bog?

A simple wetland classification categorizes these ecosystems into four basic types: swamps, marshes, fens, and bogs (Keddy, 2000). A bog is a type of wetland that accumulates peat and derives all of its water and nutrients from

rainfall. As a result of the lack of water and nutrient influx from the soil, bogs usually are nutrient deficient and have very low productivity (Schlesinger, 1978 and 1997). The plants and microbial communities adapt to these conditions and develop mechanisms to aid in their survival within a physically and chemically stressful environment. Plant communities that dominate bogs are *Sphagnum* moss, sedges, ericaceous shrubs and some deciduous shrubs (Keddy, 2000).

Plant Adaptations

Most of the plant species found in peatlands are forced to adapt to the harsh environment. Some plants adapt to conserve nutrients and develop advantageous rooting. This adaptation helps keep roots near the surface and avoid anoxic conditions (Mistch, 1993). Other species' root systems are large and deep, and help to acquire nutrients from below the peat surface and require mechanisms for the transfer of oxygen (Keddy, 2000). Still other plant species have developed ways to diffuse oxygen into the roots in order to avoid root anoxia, through the development of air spaces in the cells of the stems and roots for oxygen storage (Mitsch, 1993).

Many plants have adapted to the low nutrient environment by developing mechanisms to conserve and accumulate nutrients (Crum, 1992). Evergreen plants are able to conserve energy by holding on to their leathery leaves or allowing leaves to gradually fall off (Keddy, 2000). Many of the shrub species in bogs have tough leaves and woody stems, which allow them to tolerate the waterlogged conditions (Mitshc, 1993 and Keddy, 2000). Typically, the plants

have small leaves in an effort to conserve energy. The biomass of plants is low in nutrients and plants retranslocate the nutrients from the leaves before they senesce, resulting in low nutrient litter (Schlesinger, 1997).

Peatlands also exhibit a dominance of bryophytes. *Sphagnum* is one of the most important forms of vegetation in the bog. The moss is able to hold large quantities of water and withstand the waterlogged environment, as a result of its shoot morphology and anatomy (Limpens, 2003). *Sphagnum* also has a high cation exchange, which allows it to retain nutrients and acidify the environment (Keddy, 2000). Compounds produced by *Sphagnum* may also be attributed with the suppression of vascular plants (Keddy, 2000).

Peat Formation

Peat accumulates when the production of litter from primary production exceeds the rate of decomposition. Decomposition in a bog is slow and incomplete as a result of its complex hydrological, chemical, and topographic conditions. Bogs are waterlogged, anoxic, acidic, and cold environments (Moore and Bellamy, 1974, Chapin et al. 1980). These conditions lead to low microbial activity, which results in low rates of decomposition. The highest levels of decomposition take place on the peat surface, where oxygen is present. Further down in the waterlogged peat the conditions become anoxic, and microbes are forced to use alternative electron acceptors (Schlesinger, 1997). This anaerobic decomposition is limited and incomplete (Schlesinger, 1997).

This slow decomposition of peat leads to slower nutrient cycling. Large amounts of the nutrients get stored in the organic material, most of which is unavailable to plants because it is accumulated deep in the peat layer. *Sphagnum* moss is a dominant producer of peat because of its low nutrient supply and resistance to decomposition (Verhoeven & Liefvled, 1997). *Sphagnum* also creates the acidic and anoxic conditions, which constrain microbial activity, thus reducing the breakdown of organic matter (Berendse et al. 2001). Therefore, *Sphagnum* is vital to the peat formation and carbon storage of peatlands.

Carbon Storage:

In bogs, similarly to other ecosystems, atmospheric carbon is assimilated into plants and fixed through photosynthesis. The carbon is released back into the atmosphere by respiration of plants and the decay of organic matter. Unlike other ecosystems, peatlands have a very slow rate of decomposition, which allows organic matter to accumulate. The build up of peat leads to the storing of large quantities of carbon in the organic matter that would otherwise be released into the atmosphere as carbon dioxide, one of the gases principally responsible for climate change. Whether peatlands function as sinks or sources of carbon is dependent on whether the rate of photosynthesis is higher or lower than the rate of carbon released through respiration and decomposition (Frolking et al. 2001). The global carbon sink of peatland systems accumulates approximately one-third of the world soil carbon pool, which is greater than 100kg C/m^2, or equivalent to the amount of carbon within the atmosphere (Post, 1982 and Gorham, 1991, and

IPCC, 1990, Mitchell, 2002). Average annual carbon accumulation rates of these systems range between 10 and 30 g C $m^{-2} y^{-1}$(Turunen et al. 2002, cited in Bubier, 2003). Northern peatlands have been a sink for CO_2 over the past 5,000- 10,000 years; average carbon accumulation rates are estimated to be 0.02 to 0.03 kg C $m^{-2} y^{-1}$ (Gorham 1995; Tolonen et al.1992 sited

Sphagnum plays an important role in the carbon storage of peatlands. *Sphagnum* decomposes more slowly than the litter of vascular plants (Verhoeven and Liefveld, 1997). Vascular plants generally have higher nutrient content and less recalcitrant material (Keddy, 2000). *Sphagnum* also helps to create conditions favorable for carbon storage because of its important role ecosystem engineer and ability to produce acidic and wet conditions, which in turn strongly inhibit the microbial degradation of plant litter (Limpens, 2003). *Sphagnum* sequesters more carbon in temperate and northern ecosystems than any other group of plants (Limpens, 2003). The ability for a peatland to act as a source or sink of CO_2 is strongly dependent on the quantity of *Sphagnum* and vascular plant biomass. Greater *Sphagnum* biomass will result in more carbon sequestration within the peatland, whereas more vascular plant biomass would result in less carbon sequestered, because of the decomposability of the material.

Nutrients:

Nutrients are required by plants for growth and for the production of plant structural components, such as proteins and enzymes. The most limiting nutrients in a wetland include nitrogen (N), phosphorus (P), and potassium (K) (Thormann

and Bayley 1997). Nutrients become limiting when the requirements for maximum growth exceed the supply.

Nutrient Cycling Within the Bog

Net primary production in peatlands is limited by nitrogen or phosphorus, which results from the lack of water and nutrient influx from the soil (Bigger and Oechel, 1982 and Chapin et al., 2004). In peatlands, nutrient cycling is largely dependent on the breakdown of organic matter. The slow and incomplete decomposition, which allows for the accumulation of peat, limits the nutrient availability. Large quantities of nutrients are stored in the peat and a relatively low concentration is actually available in the soil (Schlesinger, 1997, Hemond 1983, Damman 1988). This large quantity of the total nitrogen stored in organic matter requires chemical action for conversion to usable forms. However, such conversion depends on microbial communities, as well as regeneration by rotifers, which can provide as much nutrients as rain, but are inactive under acidic conditions (Crum, 1992, Bledzki and Ellison, 2002). As a result of this limited decay, nutrient cycling in the system is limited, and elements such as N, P, and K which are chemically bound in the peat, are not released. The majority of the microbial activity is found in the first few centimeters of the peat, where oxygen is available (Schelsinger, 1997). In this peat layer, the availability of nutrients is greatest (Schlesinger, 1997). Microbes and plants are able to utilize the available nutrients, thus they are likely to be in competition for the supply (Bigger and Oechel, 1982).

Nitrogen

Nitrogen is required by all life. The atmosphere is a reservoir of nitrogen gas and contains 79 percent N in its inert form (3.9×10^{21} g N; Aber and Melillo, 2001, Galloway and Cowling, 2002, and Schlesinger, 1997). The atmospheric reservoir contains the largest pool of nitrogen. Nitrogen is also found in terrestrial biomass (3.5×10^{15} g) and in soil organic matter (95 to 140×10^{15}g) but in smaller quantities (Post et al. 1985, Batjes 1996 sites in Schlesinger, 1997). More than 99 percent of atmospheric N is unavailable to more than 99 percent of living organisms because they are unable to use the molecular form of nitrogen (Galloway et al 2003). Plants require nitrogen to be fixed into nitrate or ammonia (Aerts and Chapin 2000). As a result of plants' inability to assimilate molecular nitrogen and the substantial energy investments required to break the triple bonds of N_2, nitrogen limits primary growth in terrestrial ecosystems (Tamm, 1991, Aber and Melillo, 2001, Galloway et al., 2003).

The nitrogen cycle is one of the most important and complex global cycles. Nitrogen fixation is the process by which microbes convert inorganic, molecular nitrogen to ammonium and nitrate (Botkin and Keller, 2003). Globally nitrogen fixation supplies only 12% of the nitrogen assimilated into land plants (Schlesinger, 1997). The dominant source of nitrogen to plant communities in non-polluted regions is internal cycling of nutrients and break down of organic matter, although in cold, wet, and acidic ecosystems such as bogs, precipitation inputs are more important (Tamm, 1991, Schlesinger, 1997). Atmospheric

deposition (wet- rain, snow, aerosol; dry- dust) is the precipitation of nitrate and ammonium. This is the primary source of nitrogen to systems where the internal cycle is limited (Aber and Melillo, 2001).

The internal N cycle requires the assimilation of nitrite and ammonia from the soil into the plants' biomass. When these plants die or when the litter is deposited, they decompose, and the nitrogen from the organic matter is returned to the system. Nitrogen release is largely dependent on the C: N ratio of the litter; litter with a large supply of nitrogen decomposes more rapidly (Crum, 1992). Site fertility is largely dependent on decomposition releasing nitrogen from organic matter as ammonium, through the process of mineralization (Aber and Melillo, 2001). Once nitrogen is mineralized and available, plants and microbes compete for the nutrient. Plants are able remove nitrogen from leaves before they senesce, through retranslocation (Aber and Melillo, 2001). The process of retranslocation can be beneficial in systems with a limited nutrient supply (Crum, 1992, Meyer, 1994 cited in Schlesinger, 1997). The form of nitrogen taken up by plants has implications for the system soil chemistry. Nitrate is produced when some of the ammonium from the mineralization process is oxidized through the process of nitrification (Schelesinger, 1997, Aber and Melilo, 2001). The process of nitrification is controlled by soil pH, ammonium availability, and the presence of oxygen (De Boer et al. 1990, Schlesinger, 1997). As a result of these limitations, this process takes place in the peat surface where ammonium is available from decay. In waterlogged environments, nitrate is often reduced to nitrogen gas

further down in the anoxic portion of the peat, through the process of denitrification (Merrill and Zak 1992, Schlesinger 1994, Crum, 1992, Kirk and Kronzucker, 2005).

Nitrogen Deposition

Human activities have greatly altered the nitrogen cycle. Anthropogenic emission of nitrogen has more than doubled the inputs into terrestrial systems globally (Matson et al. 2002). The rate of atmospheric N has greatly increased since the beginning of the 20^{th} century with the invention of the Haber- Bosch process, which can create ammonia from organic N to be used as fertilizer for food crops (Galloway and Cowling, 2002, Galloway et al. 1995). This invention has lead to intensive food production following by population expansion, increased energy consumption, and further industrial activities (Galloway and Cowling, 2002). N emissions have also increased as a result of increases in fossil fuels and biomass burning (Galloway et al., 1995, Penner et al. 1991, Schlesinger, 1997). These anthropogenic inputs exceed the amount of global biologically fixed N (Galloway et al., 2003). The sources of biologically fixed N include N fixing organisms and lightening. Nitrogen fixing organisms fix an estimate of 90- 140 x 10^{12} g N/yr in terrestrial ecosystems prior to human activity, and lightning continues to produce approximately 5 x 10^{12} g N/yr (Vitousek et al., 1997; Schlesinger, 1997, Galloway and Cowling, 2002). Human fixation of nitrogen through processes of fertilizer use, fossil fuel combustion, cultivation of N- fixing crops, draining of wetlands, burning of biomass, and land clearing create a total estimate of 140 x 10

^{12} g N/yr or greater of new nitrogen added into the global systems (Vitousek et al., 1997). This human fixation of N converts organic nitrogen from the atmosphere to biologically usable forms. The release of gases and particulate matter from these processes results in the wet and dry deposition of nitrate and ammonia to the land. High rates of atmospheric N deposition have been measured in Europe (ranging from 1 to more than 75 kg N ha^{-1} yr^{-1}) and North America (13 kg N ha^{-1} yr^{-1} in Ontario, Canada, and 6- 11 kg N ha^{-1} yr^{-1} in southwest Sierra, Nevada ; Dise and Wright, 1995; Fenn et al., 1998).

Phosphorus

Phosphorus is another very important element that is required by all life. Phosphorus is essential to the basic processes in plants and is required for growth and development. It is an integral part of enzymes and nucleic acids, which are required for photosynthesis and the production of DNA molecules. Phosphorus is also a major limiting nutrient in wetlands because it is not present in a gaseous phase, and the main sources are rock weathering, water flow, and recycling (Keddy, 2000). Phosphorus limits the growth of bog plants because so little is available (Thormann and Bayley, 1997). In bogs, there is limited water flow and slow decay, which results in an inadequate supply of organic phosphates (Mitsch and Gosselink, 1993). As peat accumulates, plants become increasingly isolated from mineral P inputs and consequently depend more on the limited recycling of P bound in recalcitrant organic matter (Chapin et al. 2004). Phosphorus also

occurs in peat in mineral compounds, mainly as phosphates of aluminum, iron, and calcium.

As a result of the lack of a gaseous phase the phosphorus cycle is significantly different from the nitrogen cycle. Phosphorus exists in the atmosphere only in particulate form. The atmospheric inputs of P in precipitation are small (Schesinger, 1997). The majority of inputs into terrestrial ecosystems come from the weathering of minerals (Aber and Mellilo, 2001). Phosphorus is taken up by plants in the form of phosphate (Botkin and Keller, 2003). Generally, the phosphate that is taken up by plants is recycled when the plants are decomposed and regenerated by rotifers, but as a result of the slow decomposition in bogs, there is little phosphorus returned to the soil (Bledzki and Ellison, 2002, and Schlesinger, 1997). Plant growth depends on the release of phosphorus from organic material.

Human activities have intensified the release of P from the weathering of rocks (Schlesinger, 1997). The global mobilization of P has roughly tripled compared to its natural flows (Smil, 2000). This increase is a result of soil erosion, runoff, fertilizer use, and industrial waste discharge (15 million tonnes P/year; Smil, 2000). Phosphorus loading into water systems is a major cause of eutrophication and greatly affects marine systems throughout the world (Smil, 2000).

Potassium

Rain and snow are low in potassium content, and hence bogs are deficient in that element (Crum, 1992). Potassium (K) is essential for photosynthesis and is an important enzyme activator within plants. The cycling of potassium is very different from N and P because it is a metal cation, which moves through plants in its ionic form (Aber and Mellilo, 2001). Throughfall of water and stream flow play a large role in the cycling of potassium (Schlesinger, 1997). Throughfall is higher in potassium concentration than rain and can help to cycle potassium in a system. Overall, the potassium cycle is simple; the inputs come from precipitation and weathering (Botkin and Keller, 2003). Plants take up potassium from soil pools (Schelsinger, 1997). These pools can be affected by factors such as low ph, resulting in unavailable forms of potassium (Aber and Mellilo, 2001). Potassium easily leaches from litter and plant surfaces, which replenishes the cycle (Aber and Mellilo, 2001).

Fertilization:

The increase in atmospheric deposition threatens the structure and function of many N-limited ecosystems (Galloway et al. 2002). These ecosystems and plants have adapted to nutrient limited conditions. High rates of nutrient inputs can result in a temporary enrichment or eutrophication of ecosystems, which increases plant growth over the short-term, but over the long-term, causes a destabilization of plant communities and promotes ecosystem

decline (Aber et al. 1989). High rates of N deposition can cause other nutrients required for plant life to become limiting and cause greater nutrient imbalances.

Nutrient deposition has implications for the global carbon cycle by potentially enhancing the rate of decompositions and by potentially disrupting the balance between *Sphagnum* and vascular plants in bogs (Lamers et al., 2000, Limpens and Berendse, 2003, Limpens, et al., 2004). Sphagnum species have the ability to sequester the bulk of the carbon accumulated in peatlands because the litter is composed of materials that are resistant to microbial degradation (Berendse et al., 2001). Under low deposition, *Sphagnum* is capable of completely absorbing the inputs (Limpens et al., 2004). As the addition increases, however, the *Sphagnum* becomes N-saturated and eventually loses the ability to filter the nutrients (Lamers, et al., 2000). When the S*phagnum*'s ability to filter the N fails, the nutrients become available for vascular plants. The vascular plants are able to expand and eventually lead to declines in the moss species by shading out the light (Limpens and Berendse, 2003). An increase in the population of vascular plants affects the decomposability of litter, the system's ability to store carbon, and possibly the global carbon budget.

Biomass

Some studies have found that fertilizer can cause increases and then decreases in forest and grassland productivity. This fluctuation is a result of initial utilized deposition and followed by fertilizer increases beyond critical thresholds of the system (Vitousek and Howarth, 1991, Vitousek et al., 1997). Aber et al.

(1995) report results of chronic N additions causing declines in tree growth within the Harvard Forest pine stand and Mt. Ascutney spruce-fir system. Other studies have found positive effects of fertilizer on productivity. An increase in the overall vascular plant biomass has been observed in north-western Europe where critical deposition loads have been exceeded (Aaby, 1994, Hogg et al., 1995 sited in Limpens and Berendse, 2003). In Europe, wetlands have become more productive and shifted to species poor communities as a result of increased availability of limiting nutrients, such as N, P, and K (Olde Venterink et al., 2002, Bridgham et al. 1996). Above ground biomass is positively correlated to the amount of N available, as measured within a biomass gradient in Western Europe (Olde Venterink et al., 2002).

Carbon Assimilation

Carbon assimilation is the process by which carbon is taken out of the atmosphere and fixed by plants. Plant growth directly affects the composition of the atmosphere and the soil (Schlesinger, 1997). The rate of photosynthesis is directly correlated to the leaf nitrogen content. Leaf enzymes account for 20-30% of the leaf nitrogen (Evans 1989). The availability of N determines leaf enzyme contents and the rate of photosynthesis (Evans 1989). Reich (1968) states that low N concentrations are associated with lower mass- based photosynthetic capacity because N is required in the production of photosynthetic enzymes and pigments. As a result of the nutrient limited conditions within the bog, photosynthesis is expected to maximize with nutrient additions.

Johnson et al. (2000) presented results form wet sedge ecosystems in the Arctic after eight years of fertilization. The two sites measured showed an increase in photosynthesis in response to fertilization. The site that was more nutrient limited showed greater increases in photosynthesis in comparison to respiration, resulting in greater carbon storage within the system.

Nutrient Content and Litter Production

Carbon allocation and nutrient use efficiency determine the litter quality (Limpens and Berendse, 2003). High quality litter decomposes faster, as a result of the nutrients available for microbes to function (Aerts et al, 2001). However, when nitrogen is limiting and there is low nitrogen content in the litter, as a result of translocation, then microbial function is reduced and the decomposition of the material is also reduced.

Purpose of This Project:

Faced with a changing environment, we need to understand how species will respond. Understanding is especially important in peatland ecosystems where species composition, productivity, and decomposition can greatly affect the system's ability to store carbon with implications for the global carbon cycle. This study uses the addition of NPK at Mer Bleue bog, located in Ottawa Ontario, to assess the relative importance of elements that control plant growth. The experimental application of nutrients illustrates the potential changes in vegetation with atmospheric deposition.

The objective of this study is to gain insight into how increased atmospheric deposition of nutrients will affect vascular plant communities. Observed changes resulting from the fertilization at Mer Bleue include a loss of *Sphagnum* and *Polytrichum* within the higher nutrient treatments (Basiliko, 2004). In order to understand the cause of these changes within the moss communities and the future of the system's ability to sequester carbon, it is necessary to study the vascular plants.

We hypothesize that vascular plant biomass will be enhanced by the higher levels of fertilization. This increase in biomass is expected because the plants are no longer limited by nutrients, allowing the allocation of energy to the production of biomass and leaves. Plants in elevated nutrient treatments will have taller and denser canopies. These plants will no longer be under the stress of nutrient limitation and may have the ability to increase their growth.

We expect to see a positive correlation between levels of nutrient addition and carbon assimilation (Vmax). Vmax, which is the photosynthetic rate under optimal external conditions, may be greater at high nutrient levels. Plants in high nutrient conditions are no longer constrained by nutrient limitations and the only factor that will limit the maximal photosynthetic rate is the concentration of rubisco in the leaf (Lambers et al., 1998). The fertilizer addition may allow plants to enhance the chlorophyll and rubisco content within leaves and resulting in increased rates of photosynthesis. Chlorophyll and rubisco require nitrogen for

their production and under high N conditions more of these compounds could be produced.

We hypothesize that LAI (leaf area index) will be positively correlated to increased concentrations of fertilizer addition. Higher levels of fertilization may produce leaves with a larger Leaf Area Index (LAI) in the canopy. The larger leaf surface area will enhance productivity, efficiency, and increase access to sunlight.

Similarly, we hypothesize that higher levels of fertilization will be positively correlated with low C: N of leaves**.** In the high fertilizer treatment the C: N ratio is expected to decrease because there will be more nitrogen available for plants to take up. In the low fertilizer and control treatments the C: N ratio is likely to be high because nitrogen is a limiting factor.

We expect the treatments with higher levels of fertilization will produce a larger concentration of litter (cover and mass). Nutrient addition may lead to greater quantities of dead biomass, resulting from an increase in biomass and biomass turnover. Plants will be able to turnover biomass more rapidly because of the addition of nutrients, allowing them to be less conservative. Litter may also increase as a result of increased foliar biomass.

MATERIALS AND METHODS

Site Description

Field work for this project was completed from May to August of 2005 at Mer Bleue, a cool temperate peatland located 10km east of the city of Ottawa in the Ottawa River Valley (45.40º N lat., 75.50º W long.). Mer Bleue is a large ombrotrophic bog approximately 24km^2 in size (Moore et al., 2002). Mer Bleue is part of a long term research site that was established in 1997 as part of Fluxnet-Canada, a national research network created to study the future of carbon storage in Canadian ecosystems. Mer Bleue has one of the longest records of carbon accumulation and net ecosystem exchange. Annual sequestration of CO_2 measured at Mer Bleue is approximately 70–80 g CO_2 C $m^{-2}yr^{-1}$.

Mer Bleue is dominated by low shrubs consisting of *Chamaedaphne calyculata* (Leather Leaf), *Ledum groenlandicum* (Labrador Tea), and *Vaccinium myrtilloides* (Blueberry). Other species present in the bog include: *Vaccinium oxycoccus* (Cranberry), *Eriophorum vaginatum* (Cottongrass), *Carex trisperma* (Three-Fruited Sedge), *Smilacina trifolia* (Solomon's seal), *Kalmia polifolia* (Bog Laurel), and *Kalmia angustifolia* (Sheep Laurel). Dominant moss species present in the bog are *Sphagnum magellanicum*, *Sphagnum capillifolium*, and *Polytrichum strictum.* Bubier et al. (2005) measured aboveground biomass with an average of 591 g m^{-2} from within the bog area where this study was performed. Bubier et al. (2005) also showed a dominance of shrub biomass and *Sphagnum* mosses within the transects measured at the bog. *Ledum* (37% of total biomass)

and *Chamaedaphne* (24-27% of total biomass) were the dominate shrubs measured near this study site.

Fertilization

The fertilization experiment was established at Mer Bleue in 2000 with six different treatments each with three replicate plots. Additions are ongoing to the present time. Overall, the experiment is composed of 18 three by three meter plots. Nutrients are added in dissolved form with 2mm of water (2 L m^{-2}) at three week intervals from May to early September. Nutrient addition of N is based on an estimated ambient summer loading of 0.3g N m^{-2}, and the PK application is similar to that used in other peatland fertilization experiments. PK is added to reduce the nutrient limitation, there by allowing the N addition to affect growth. The treatments include a control (receives only distilled water), PK (receives 6.3g Pm^{-2}, 5.0g K m^{-2}), 5N (receives 1.6g N m^{-2}), 5NPK (receives 1.6g N m^{-2} Pk, which is 5x the summer ambient loading of N), 10NPK (receives 3.2g N m^{-2} PK, which is equivalent to 10x the summer ambient loading of N), and 20NPK (receives 6.4g N m^{-2} PK and is equivalent to 20x the summer ambient loading of N; See table on next page).

Fertilization additions:

Treatment	**Nutrients**
20NPK (20x)	6.4g N m^{-2} PK
10NPK (10x)	3.2g N m^{-2} PK
5NPK (5x)	1.6g N m^{-2} Pk
PK	6.3g Pm^{-2}, 5.0g K m^{-2}
5N	1.6g N m^{-2}
Control	Distilled H_20

Vegetation Measurements

I conducted field measurements with the assistance of students from McGill University. We measured vegetation through non-destructive and destructive sampling methods. In each of the 18 plots there are aluminum collars in place for continuous NEE (Net ecosystem CO_2 exchange) measurements using the static chamber method (Bubier et al. 2003). As a result of the long term nature of this research site, it was not possible to clip and weigh the vegetation inside the NEE sampling collar to determine biomass. Instead we measured the stem height and density to provide an inferred biomass value. Within each collar we used a 60 x 60cm quadrat, divided into 36 equal 10 x 10 cm squares to estimate biomass. Within each square, we recorded the average stem height and stem number for each species. We separated data (density and height) for plants shorter than 5 cm and recorded them separately from the taller plants. Total stem

number x average stem height for each species and each plot offered an estimate of species specific biomass. We also recorded moss and litter coverage for each plot by estimating a total percent cover for the collar area. We took all measurements once from June to August on all of the plots.

We collected destructive vegetation samples from outside the NEE collar for each plots. We clipped three samples each of *Chamaedaphne calyculata* (Leather Leaf), *Ledum groenlandicum* (Labrador Tea), and *Vaccinium myrtilloides* (Blueberry), for a total of 54 plant samples from all 18 plots. We clipped the plants down to the peat surface, placed the samples in plastic bags, and stored them on ice until they were measured. We collected each of the species on the same day to limit variability. The plants were selected from within the plot. We did not sample from within the NEE sampling collar (to limit disturbance) or within the 1m perimeter along the edge of the plot (to reduce edge effect). For all of the clipped plant samples we measured the number of leaves, number of small leaves (less than 1cm), number of stems, stem length, total plant height, number of leaves per stem, and leaf length. After we completed the measurements, we dried and weighed the plants.

We used the measurements of plant characteristics from the clipped samples to estimate the amount of woody and foliar material for each plant. Estimating was necessary because we did not take biomass measurement of stems and leaves. These data are important in order to determine how biomass is changing and to understand how plants are allocating their resources (producing

more woody or foliar material). The first step in this process was to calculate the foliar estimate. The foliar estimate was equal to the total number of leaves on the plant multiplied by the average leaf length ($Leaf\,\# \times average\ leaf\ \ size$ = Foliar estimate). The leaf length was an average of the 10 – 20 leaves measured from the plant. We did not measure the length of all the leaves because some plants had such a high density of leaves. Also, we only measured the leaf length because we did not expect the ratio of leaf length: width to change. This calculation provided an estimate of leafy matter (the size of individual leaves average of the measured leaf length and the sum of leaf length for the plant). The second step was to calculate a woody estimate. The woody estimate was equal to the number of branches multiplied by the sum of branch length plus the plant height ($\left(\#\,Branches \times sum\ branch\ lenght\right)$ + *Plant height).* This calculation allowed offered an estimate of the plant's woody material. Finally, both of these estimates were used to calculate a foliar: woody ratio for the treatments.

These estimates assume a direct correlated between the leafy and woody volume and the plant's leafy and woody biomass. They do not take into account the change in leaf mass with nutrient addition and the difference in mass of woody and foliar material. However, they do help to identify changes in plant growth (i.e. bushier, taller) by offering information about the relative changes in volume allocations to leafy vs. woody material among treatments.

Carbon Assimilation

We studied carbon assimilation in three of the dominant species: two primary ericaceous shrubs and a deciduous shrub. Ericaceous shrubs belong to the family Ericaceae and usually have thick, leathery, and evergreen leaves (Newmaster et al., 1997). In contrast to evergreen plants, deciduous species lose their leaves annually.

We collected measurements of light and CO_2 response curves using an open infra-red gas analyzer (IRGA) system (Li-Cor 6400). These measurements show how different species respond to varying levels of PAR and CO_2 concentration when all other factors are held constant. The data from the response curves is used to calculate the maximal photosynthetic capacity (Vmax) for the different species within the treatments. We measured *Chamaedaphne calyculata* and *Ledum groenlandicum*, only in the 20NPK and control plots, and all during the month of August. We measured light and CO_2 response curves for Vaccinium mostly in the 20NPK and control plots, sporadically throughout the summer with the majority of the measurements completed in July (however, the data were insufficient for analysis). We selected plants within the plot for these measurements. We calculated the cumulative mean photosynthetic rate for each species from the initial Li-Cor 6400 measurements. We took multiple measurements for each species and, based on the variability of the cumulative mean graphs, determined the minimum number of leaf measurements needed to calculate V_{max} (Figures 1 2, and 3). This method helped to produce data with

lower variability and allowed us to determine that we needed Li-Cor 6400 measurements for a minimum of six leaves per plot and per species. To limit disturbance, we did not measure plants within the collar, and to avoid edge effect we did not measure plants within a one meter border along all sides of each plot. The Li-Cor 6400 measures light and CO_2 response curves by fluctuating PAR (photosynthetically active radiation) as well as the concentrations of carbon dioxide within the sample chamber. During light response curve measurements, all other variables, such as humidity, flow, and carbon dioxide, were constant as PAR decreased from 2,000 to zero umol photon m^{-2} s^{-1}. We set carbon dioxide above the CO_2 saturation point, which for all of the plants measured was 1200 ppm (as suggested by Li-Cor manual). The machine collected measurements at eight different light levels throughout one run. A CO_2 response curve was developed similarly to the light curves, with PAR, humidity, and flow held constant as the CO_2 concentrations varied within the chamber. PAR was set above the light saturation point for all of the CO_2 response curves (1300 umol photon m^{-2} s^{-1}). The light saturation point was determined by preliminary light response curves measured for each species. Measurements were logged at 13 different concentrations ranging from 400 to 2000ppm. Determining the saturation point for CO_2 response curves was more difficult than the light curves. This is a result of the sampling variability and the possibility that, even when photosynthesis has reached its saturation point, the net carbon exchange is still increasing (Elliot, 2004). Measurements were collected on *C. calyculata* and *L.*

groenlandicum, however, the variability in the *L. groenlandicum* runs was too great to estimate the saturation point. For all of the response curves measured the chamber temperature was set at 25 degrees C°, sample humidity was set at 16 mmol mol^{-1}(average ambient conditions), and the flow air was monitored to stay round 150 ppm by adjusting the desiccant.

After the Li-Cor 6400 measurements were complete, we took digital photographs of each leaf with a ruler in the frame to maintain an accurate scale. We used ImageJ to calculate leaf area from these photographs. ImageJ is a program developed by Wayne Rashband at the Research Services Branch, National Institute of Mental Health, Bethesda, Maryland, USA. The program is a public domain Java image processor. The leaf areas were used to recompute the data (from light and CO_2 response curves) collected with the Li-Cor 6400 by using the Li-Cor Simulator program. This correction of the data was necessary because the Li-Cor determines the gas flux based on the appropriate leaf area.

Leaf Area Index (LAI)

Leaf area index is the ratio of leaf area to unit area of ground (Licor, 2005). Basically, LAI is the area of leaf surface divided by the area of ground. Sylvain Leblanc from Canada's Natural Resources Centre for Remote Sensing, measured leaf area index using the Li-Cor 2000. The Li-Cor 2000 measures LAI by measuring the difference in light levels through the canopy. Sylvain took measurements above and below the canopy to determine the light extension, from which LAI was computed (Li-Cor, 2005). Sylvain took multiple measurements

from within each plot, once during the growing season. All the measurements were completed in one day to limit the effects of changing light condition and minimize variability.

C: N Analysis

We performed C: N analysis on the clipped vegetation samples from each treatment. We oven-dried the samples, ground them using a Wiley Mill, and then stored the ground material in an 18 ml plastic vile. We then sent the samples to GEOTOP laboratory at McGill University to be analyzed.

Litter

In order to quantify changes in litter abundance between treatments we estimated litter cover and collected litter samples from the 18 plots. We estimated percent cover of litter within the NEE sample collar and outside the collar. We only collected litter samples from outside the NEE sample collar. We used the quadrat to help separate the area and determine an overall percent litter cover for the collar. We then placed the quadrat randomly at three spots in the plot, estimated the percent cover of litter, and collected litter for one square each time (10 x 10 cm). We labeled the square, and for each litter sample we used the same square. We then dried the samples (three litter samples per plot for a total of 54 samples) in an oven and then weighed the litter samples.

` STATISTICAL ANALYSIS

With the help of my advisor Martha Hoopes and Leszek Bledzki, I performed statistical analysis on the data. We conducted all statistical analysis using SPSS Graduate pack 13.0 (SPSS Inc. Chicago, IL, USA) with an alpha level of 0.05 for all analyses. For many of the questions we used ANOVA to look at overall treatment effects and regression to look at trends in effects with increases in NPK addition, thus only using the control, 5NPK, 10NPK, and 20NPK data (0, 5, 10, and 20 as the independent regression variables). All ANOVA test used a Tukey post hoc comparison to determine the differences between treatments. For all tests we tested for normality. If transformations were necessary we mention them in the related section. For all graphs we used the standard deviation for the error bars.

Vegetation Measurement

Estimated Biomass

We conducted a one-way Analysis of variance (ANOVA) to test fertilizer affects on the estimated biomass (stem height x density) for all of the treatments and for just the elevated NPK and control treatments. We used a Tukey post-hoc test to determine the difference in biomass between treatments.

We also performed linear regression on these data, to determine if there was a directional trend. The dependent variable was the estimated biomass, and the independent variable was the squared elevation for each treatment (20^2, 10^2,

5^2, and 0^2). For this analysis we excluded the PK and 5N plots in order to identify the effect of NPK elevation. We squared the independent variable in order to fit a quadratic to the data.

Biomass (clipped plant samples)

For the clipped plant biomass we performed analyses similar to those for the estimated biomass. We used a linear regression to examine the relationship between the total biomass (sum of three samples) versus treatment. We used ANOVA to determine if there was an effect of nutrient addition on the total biomass and the biomass of the individual plant species. Additionally, regression analysis was used on these data to test the relationship between fertilizer addition (of elevated NPK and control plots) and biomass for *Chamaedaphne, Ledum*, and *Vaccinium.* The dependent variable for the regression was the biomass and the independent value was the treatment value (0, 5, 10, or 20). For some analyses we also added the squared treatment value in order to fit the data to the quadratic.

Clipped Plant Measurements

First we used an ANOVA to determine the effect of nutrient addition on the number of leaves, leaf length, and number of branches, branch length, and plant height. Then, we used linear regression to examine the relationship between nutrient addition (for elevated NPK and control plots) and the number of leaves, leaf length, and number of branches, branch length, and plant height. The dependent variable was the measure of the plant characteristic and the

independent variable was the treatment value. For some of the analyses it was necessary to add a squared term to the regression in order to fit data.

The foliar estimate is an approximation of leaf material from the clipped plants ($Leaf\,\# \times average\ leaf\ \ size$ = Foliar estimate) and the woody estimate is an approximation of total amount of woody material ($\left(\#\,Branches \times sum\ branch\ lenght\right)$ + *Plant height).* We analyzed both of these estimates separately through the use of ANOVA and regression. Then, we calculated the ratio of the foliar: woody estimates and performed analyses on these data. We used an ANOVA to determine the effects of nutrient addition on the ratio. We used a linear regression to test the relationship between the foliar: woody estimate and nutrient addition for the elevated NPK and control plots (the independent variable was the treatment value and the dependent was the ratio estimate).

Carbon Assimilation

We performed independent sample t-tests on the estimates of the maximum photosynthetic rate (V_{max}) for the control and 20NPK treatments. The data were an average of the V_{max} values calculated for each of the measurements for the particular plot and species.

Leaf Area Index

We analyzed leaf area index using a one-way ANOVA with a Tukey post-hoc comparison to determine the differences in leaf area within the various treatments.

C: N

We transformed the C: N data using an arcsine transformation (= $2\ arcsine\left(\sqrt{N:C}\right)$); this required the reverse proportion in order for the values to be less than one and the calculation to be possible. The data were analyzed using an ANOVA and a linear regression. The ANOVA was used to test the effects of nutrient addition on C: N ratio for all of the treatments. The regression was used to test the relationship between C: N and the elevated NPK and control plots. The dependent variable was the transformed N: C ratio and the independent variable was the treatment value (0, 5, 10, and 20).

Litter

Litter cover data were transformed into the Van der Maarel (1979) 8-point cover classes (based on cover values 0.1, 1, 2, 5, 25, 50, 75 and 100) and I then analyzed the data with a one-way analysis of variance. I also analyzed the litter mass data using a one- way ANOVA. All analyses used a Tukey post-hoc comparison to determine the difference in litter between treatments.

RESULTS

Vegetation Measurements

Estimated Biomass

These data are an estimate of biomass using the measured stem density and average height of the plants. There was no statistically significant difference in the estimated biomass among the six different treatments; Figure 4 shows the bar graph for the estimated biomass data (Table1 and 2). Most of the difference in vegetation was expected in the NPK treatments (20NPK, 10NPK, and 5NPK). We used regression analysis to test for a positive correlation between the control and biomass estimate. A scatter plot of biomass estimate versus NPK and control treatment shows an increase in stem height x density through 10NPK with a drop at 20NPK (Figure 5). The regression analysis indicates a significant relationship between the squared NPK treatment and the estimated biomass.

Biomass

We found the highest biomass in the 20NPK (average of 12.9 g ± 4.4) and 10NPK (average of 10.3g ± 1.01) plots, and the lowest in the control plot (average 5.036 ± 1.01), with a marginally significant effect of nutrient addition (Figure 6 and Table 3). These data differs from the estimated biomass measurements and shows a linear relationship with nutrient addition. A regression shows that this is a significant relationship (Table 3). Figure 7 shows the scatter plot of the elevated

NPK treatments and the control. The graph shows significant increase in biomass from the control to the 20NPK treatment.

We used similar analyses for *C. calyculata, L. groenlandicum*, and *V. myrtilloides* to determine whether nutrient addition affected the biomass of the individual species. Biomass of *C. calyculata* was significantly greater in the 10NPK treatment (Table 3, Figure 8) and *C. calyculata* showed a positive relationship between biomass and treatment (Table 3). Figure 9 shows the average biomass measurements for the elevated NPK and control plots because of the quadratic curve in the data we added a squared treatment value in the regression analysis. There was also a significant effect of treatment on biomass in *L. groenlandicum*. The 20NPK had significantly higher biomass than the 5NPK plants (Figure 10 and Table 3). *Ledum* also showed a significant linear relationship between biomass and elevated NPK (Figure 11, Table 3). *V. myrtilloides* biomass fluctuated between treatments, and, unlike *L. groenlandicum* and *C. calyculata* there, was no significant effect of nutrient addition (Table 3, Figure 12). However, the regression did show a significant relationship between biomass and the elevated NPK and control treatments (Figure 13, Table 3).

Figure 14 shows the average biomass for each replicate plot of the three species from the control to the elevated NPK plots. The graph shows all three of the species in a similar range. As nutrient addition increase the plants biomass becomes more variable. The graph also shows that not one of the species

consistently dominates or is responding more to the nutrients than the others. This could also be a result of the small sample size.

Clipped Plant Measurements

The clipped plant measurements indicated changes in plant growth characteristics with treatment. The plant height measurements showed a positive relationship with the elevated NPK and control plots for *Chamaedaphne* and *Ledum* (Figures 15 and 16, Table 4). For both of these species plant height significantly increased from the control (average height 18.37± 3.2 and 18.5±2.42 for *Chamaedaphne* and *Ledum* respectively) to the higher NPK plots (20NPK average height 29.24± 3.64 and 33.85±8.06 for *Chamaedaphne* and *Ledum* respectively; Table 4). The plant height measured for *Vaccinium* increases from the control but drops at the 20NPK plot. An added squared term (treatment value) was used in this regression in order to fit the data. The analysis showed a positive relationship between plant height for *Vaccinium* and treatment (control and elevated NPK plots; Figure 17, Table 4).

The number of leaves (average number of leaves for the three clipped plant samples) showed a positive linear relationship with the control and elevated NPK plots, for *Chamaedaphne, Ledum,* and, *Vaccinium* (Figure 18, 19, and 20, Table 5). There was a significant increase in the number of leaves with higher levels of NPK fertilization. However, the average leaf size (sum of leaf length divided by the number of leaves measured) showed no significant relationships

with the control and elevated NPK plots, for any of the species measured (Figures 21, 22, and 23, Table 6).

Figures 24, 25, and 26 show the number of branches for *Chamaedaphn,e Ledum,* and *Vaccinium* respectively. The numbers of branches for *Chamaedaphne* and *Vaccinium* did not significantly increase with additions of fertilizer (Table 7). The graph for *Chamaedaphne* does show a slight increase between the 20NPK and the control, however, it is not significant. *Ledum* did show a significant relationship between the number of branches and fertilizer treatment (Figure 25, Table 7). The three species showed a positive relationship between nutrient addition (for elevated NPK and control plots) and branch length (Figure 27, 28, and 29, Table 8). The number of branches for *Chamaedaphne* increases from the control but drops slightly at the 20NPK, however the number of branches is still significantly greater than the control (Figure 27). As a result of this decline in the number of branches measured in the 20NPK for *Chamaedaphne,* an added square term was used in the linear regression in order to fit the data. Overall, the average branch length for each species significantly increased with elevated fertilizer additions.

The three species measured demonstrate a relationship between foliar estimate and elevated levels of nutrient addition. *Chamaedaphne* showed a marginally significant trend (p-value 0.063) between elevated levels of nutrient addition and foliar estimate (average leaf size multiplied by the number of leaves;

Table 9). The increase in foliar estimate from the control to the 20NPK is displayed in Figure 30. The foliar estimate for *Ledum* also increased with higher levels of NPK addition (Figure 31, Table 9). Vaccinium also showed a significant relationship with the foliar estimate and increased levels of NPK addition (Figure 32, Table 9). The regression analysis for *Ledum* and *Vaccinium* indicated a significant relationship between the woody estimate and the treatments, however, the regression analysis for *Chamaedaphne* showed no significant relationship (elevated NPK and control, Figures 33 - 35, Table 10).

The foliar and woody estimates were used to calculate a ratio of foliar: woody material. The regression analysis for the three species showed no significant trend between the woody: foliar estimate and treatment (Figures 36, 37, and 38, Table 11).

Carbon Assimilation

The cumulative mean analysis helped to determine the number of leaves necessary to measure in order to ensure that measurements captured the range of variability. Photosynthesis for the three species stabilized at different levels. An example of mean photosynthetic rates for light curves measured in the control plots are in Table 12. The PAR value at which the leaves reached saturation varied between species. *C. calyculata* and *V. myrtilloides* reached light saturation at approximately the same PAR level, about 700 µmol photons m^{-2} s^{-1}. Photosynthesis stabilized at a higher level of PAR for *L. groenlandicum,* about

1100 µmol photons m^{-2} s^{-1} with a mean photosynthetic rate of 17.3 µmol m^{-2}leaf s^{-1}. The photosynthetic rates for *C. calyculata* and *V. myrtilloides* were lower with a mean of 12.8 and 9.2 respectively. The average maximum photosynthetic rate for *L. groenlandicum* in the control plots (based on light response curves) was higher than in the 20NPK plot (Figure 39, Table 13). The average photosynthetic rate for *C. calyculata* in the 20NPK plot was slightly higher than the control plots but not significantly, with a value of 22.05 µmol m^{-2} leaf s^{-1} measured in the 20NPK plots (Figure 40, Table 13).

The CO_2 response curve was similar to the light curve with an increase in the photosynthetic rate until a threshold where the rate slows (Figures 41 and 42 are examples). We recorded CO_2 response curves for *C. calyculata* in the 20NPK and control plots. Based on these data, the average photosynthetic rate within the control plot was 13.8 µmol m^{-2}leaf $^{-1}$ s^{-1} , and the saturation point was approximately 800 µmol photons m^{-2} s^{-1} for most of the runs. The photosynthetic rate in the control plots was more than double the rate of the 20NPK plot, which was 4.9 µmol m^{-2} leaf s^{-1}(Figure 43). Statistical analysis showed that this difference between the photosynthetic rate within the control and 20NPK plot is significant (Table 13).

Leaf Area Index

Fertilizer addition significantly altered leaf area index. Leaf area index was significantly greater in the 20NPK plots than the control plots (Figure 44). LAI in the 20NPK plots was also greater than LAI in the PK plots. The leaf area

increased from 2.3 ± .3 m^2 leaf/ m^2ground measured in the control plot, to 3.95 m^2 leaf/ m^2ground in the 20NPK plot. Leaf area increased with higher levels of nutrient addition.

C: N

N: C ratio significantly increased with nutrient addition for *Chamaedaphne* and *Ledum* but not for *Vaccinium* (Figure 45-47, Table 14). The increase in the N: C ratio with nutrient addition is equivalent to a decrease in the C: N ratio.

Litter

The litter mass data showed that the 20NPK treatment (mean= 4.6, sd= 2.6) has a significantly greater quantity of litter than the other plots (Figure 48, Table 15). The percent cover of litter in the 20NPK plots is significantly greater than the control and that the control has significantly less litter than all of the NPK treatments (Figure 49 and 50, Table 15).

DISCUSSION

The results of this experiment are important in understanding how nutrient limited ecosystems will respond to global change. The changes in the vascular plant community will greatly affect the ecosystem's productivity and the decomposition rates and thus affect the systems ability to store carbon.

Biomass

Both measures of biomass (estimated and biomass from the clipped plant samples) show a significant positive relationship between biomass and nutrient addition. This increase in biomass suggests that plants are no longer limited by nutrients, allowing for the allocation of energy into the production of woody and foliar biomass. Plants in the control plots are under the stress of nutrient limitation. Nutrient limited plants conserve energy by slow growth and low productivity (Crum, 1992). We expected that nutrient addition would allow plants to be more efficient at catching light, resulting in taller plants with more woody and foliar biomass. Nutrients required for growth are readily available in the high fertilizer treatments; the plants no longer need to adapt to a low nutrient supply by conserving and accumulating nutrients.

The woody and foliar estimates show differences in the amount of woody and foliar material with nutrient addition. The estimate of total foliar material indicates an increase with nutrient addition, as a result of an increase in the number of leaves. The woody estimate indicates a significant increase with the addition of nutrients for *Ledum* and *Vaccinium*. The foliar: woody ratio shows no

difference with nutrient addition thus, the data shows no shift in the allocation of nutrient towards woody or foliar material. It is possible that the estimates do not accurately portray changes in foliar or woody biomass. The estimates provide the total volume of woody or foliar material measured and do not take into account changes in branch thickness or changes in mass.

Plant height and branch length increase for the three species measured: *Chamaedaphne*, *Ledum*, and *Vaccinium* with nutrient addition. This shows that plants are becoming taller, and making longer branches. The number of branches is also increasing with the addition of fertilizer for *Ledum*. Plants are not only becoming taller and making longer branches but they are also producing more branches with fertilizer addition. *Chamaedaphne* also shows an increase in number of branches in the fertilizer treatments; however, the difference is not significant, potentially because of the small sample size.

The leaf measurements from the clipped plants show no significant difference in the leaf size (leaf length) with treatment. From these data, plants are not expanding their leaf size with the addition of fertilizer. However, the number of leaves increases for the three species measured (*Chamaedaphne, Ledum*, and *Vaccinium*) with the addition of fertilizer. Plants are producing more leaves but not altering the size of the leaves in the fertilizer treatment.

We would expect that nutrient addition would increase plant biomass, largely in the form of woody biomass, as a result of the measured increases in plant height and branch length. The data however, did not show a shift in the

foliar: woody ratio. Plants are not producing more woody material than foliar material but plants are becoming taller, bushier (increase in branch length and number), and leafier within the fertilizer treatments.

Stem elongation is a typical response of plants grown in high density conditions. It allows plants to overtop their neighbors and gain access to light (Gurevitch et al. 2002). In the untreated plots plants are unable to become taller as a result of the nutrient limitation and the cost associated with increased stem growth (Gurevitch et al. 2002). Stem elongation would be a competitive advantage for plants growing in the bog. These plants are generally very condensed and if they can grow up and gain access to more light, the plants might have the ability to out compete their neighbors.

Previous research near Toolik Lake at the artic Long Term Ecological Research (LTER) site in Alaska has also observed an increase in woody biomass with nutrient addition (Shaver and Chapin, 1980, Shaver et al. 2001, Bret- Harte et al. 2001, Bret- Harte et al. 2002). Fertilization (with 10 g /m^2 N and 5g/ m^2 P) increased the stem biomass of three species measured (*Betula*, *Salix*, and *Ledum;* Shaver et al. 2001, Bret- Harte et al. 2001, Bret- Harte et al. 2002). Overtime the fertilization experiment found a decline in plant diversity, with the increases in biomass almost entirely by the growth of *Betula nana,* while other shrubs declined in their abundance (Chapin and Shaver, 1996; Shaver et al. 2001; Bret-Harte et al. 2001; Bret- Harte et al. 2002). *Betula* shaded out other plants with a denser and taller canopy, which resulted in a loss of species diversity (Chapin and

Shaver, 1996; Shaver et al. 2001; Bret- Harte et al. 2001; Bret- Harte et al. 2002). The increase in *Betula* with fertilizer addition was mostly attributed to the increase in relatively inactive woody stem mass (Chapin and Shaver, 1996; Shaver et al. 2001; Bret- Harte et al. 2001; Bret- Harte et al. 2002). This site is more productive in comparison to Mer Bleue, it has high leaf turnover, higher nutrient uptake rates and higher leaf nutrient content. The fertilization experiment has also been taking place for the last 15 years, and on different plant species, which could create some of the differences in the loss of species diversity at the Toolik Lake site.

Carbon Assimilation

Fertilization is generally expected to increase the rate of carbon assimilation. Enhancement in the maximum rate of carbon assimilation is expected to occur when plants are no longer nutrient limited and the only factor limiting the rate of photosynthesis is the concentration of ribulose biphosphate within the leaf (Lambers et al., 1998). The fertilizer addition is expected to enhance the chlorophyll and rubisco content within leaves, increasing the rate of photosynthesis because these compounds require nitrogen and are necessary in converting light energy into chemical energy (Elliot, 2004). However, we did not find that fertilizer addition enhanced the rate of maximum photosynthesis.

The results indicate that leaf level carbon assimilation decreased with nutrient addition for *Chamaedaphne* and *Ledum*. The results show a down regulation of carbon assimilation from the control to the 20NPK plots. Down

regulation is a shift in the leaf's response curve, which results in a decreased level of carbon assimilation.

Down regulation could be caused by water or salt stress. Stomatas allow CO_2 to diffuse into the plant and also allow water and oxygen to diffuse out of the plant. Plants transpire large amounts of water, and, when plants experience drought conditions, the stomates close in order to limit water loss (Gordon et al., 1999). Similarly, plants that are under salt stress reduce transpiration through stomatal closure. The decreased stomatal conductance of these scenarios results in lowered rates of carbon assimilation (Parsad, 1997). However, these factors are probably not the cause of the observed down regulation in this waterlogged environment because the plants showed no sign of water or salt stress (wilting leaves).

Down regulation can also be caused by the limitation of other micro nutrients, such as manganese, magnesium, chlorine, or calcium. These nutrients are required during the process of photosynthesis. Manter et al. (2005) discusses the curvilinear response of photosynthesis possibly attributed to a resistance in the diffusion of carbon dioxide, a decline in rubisco content, or a reduction in activated rubisco. Declines in rubisco content can result from low P content or high carbohydrate content and could disturb photosynthesis. With fertilizer addition Manter et al. (2005) found increasing amounts of inactivated rubisco of Douglas-fir trees. They attribute this decline to increases in Mn: Mg with increase in foliar N. Mn is required to activate photosynthesis; however, Mg

competes with Mn for binding to rubisco and results in the production of inactive rubisco. The decline in activated rubisco could also have been caused by a reduction in other nutrients, such as P (Manter et al., 2005).

It is not clear as to whether plants are experiencing toxic fertilizer effects because we have measured a positive relationships to biomass. There is also no sign of plant stress in the plots. The possible cause of this down regulation could be the allocation of nutrients to other parts of the plant, such as the woody biomass but this is not supported by the data. We expected this shift in allocation because of the increased plant height, branch length, and the visible differences of plants in the elevated fertilizer treatments. Alternatively, the decline carbon assimilation within the fertilizer treatments could be result of some other nutrient limitation. Phosphorus is limiting in the fertilization plots as a result of high N addition. Phosphorus is required for the process of photosynthesis and could be a factor in the down regulation.

This anomaly of increased growth and decreased leaf photosynthesis was found for heather and bracken within fertilization treatments in northeast Scotland (Gordon et al., 1999). Bigger and Oechel (1982) found results of down regulation of carbon assimilation in response to NPK fertilization. The contradicting results between photosynthesis and biomass with fertilizer addition have also been attributed to changes in allocation patterns (Chapin and Shaver 1996, Gordon et al., 1999). Gordon et al. (1999) suggest that the energy storing sugars produced

during photosynthesis are being allocated towards shoot and structural growth, which is very similar to our results.

Elliot (2004) measured similar photosynthetic rates at Mer Bleue during the summer of 2004. Although, these measurements were not collected in the fertilization plots, they provide a reference for the control measurements and prove to be comparable.

Leaf Area Index

LAI is a nondestructive method of obtaining an estimate of biomass. It measures the amount of light emitted through the canopy. These measurements increase with fertilizer addition. However, these results are a product of a denser canopy, which allows less light to penetrate within the fertilizer treatments. This denser canopy is not a result of increased area but rather an increase in the number of leaves and changes in plant growth with increases in woody biomass. The increase in LAI is essentially an increase in shadiness. The increase in woody biomass is producing taller plants with a greater number of long stems, which would allow plants to grow less condensed and effectively block light from entering through the canopy.

C: N

The carbon to nitrogen ratio comes from the percent of carbon and nitrogen measured within the leaves. Plants from the control plots show a high C: N ratio because N is limiting and there is a high concentration of C within the plant structural material. In the fertilization plots the C: N ratio decreases as the

concentration of fertilizer increases. This decrease is a result of the increased N available to the plants. It proves that the plants are taking up the nitrogen that is added to the plots. This will greatly affect the decomposition rates of the plant material by possibly leading to the production of higher quality litter in the treatment plots.

Litter

Litter mass and percent cover with positively correlated with fertilizer addition. The fertilizer plots have higher build up of litter, which is a result of 5 years of accumulation, sine the commencement of this may be a product of the increase in number of leaves which could lead to greater quantities of dead biomass. Also, there could be a greater biomass turnover with the addition of nutrients, allowing plants to be less conservative

Johnson et al. (2000) also found a large increase in litter after 8 years of fertilization. The litter mass was shown to double in the fertilization treatments along with plant cover and gross productivity. This increase in litter will have important implications for decomposition and carbon storage within the system. Vascular plant litter is decomposed readily and with the possible increase in nutrients available to microbes, it could lead to increased decomposition and loss of C.

CONCLUSION

In conclusion the treatment effects at Mer Bleue are producing an increase in biomass. This increase appears to be of plants allocating the available nutrients to stem growth, branch length, and number of leaves. With nutrient addition plants are becoming taller and are producing a greater number of longer branches. In the future, this increase in plant height might create competition for light between the plant species and eventually lead to a decline in species richness and a possible shift in dominant species. Similar outcomes of fertilization were observed at the Toolik Lake site and eventually produced a decline in plant diversity (Shaver et al. 2001, Syndonia Bret- Harte et al. 2001, Syndonia Bret-Harte et al. 2002)

Plants are also producing a greater number of leaves. This might also be related to the increase in branch length providing more places for leaves to grow. Even though there are more leaves, these leaves are assimilating less carbon. Leaf level carbon assimilation has decreased but total plant assimilation might not decline, especially with the production of more leaves. However, total gross photosynthesis measured in 1 x 1m collars within the plots also shows a decrease with increasing fertilizer addition (Bubier et al. 2005, in progress). Plants may be reducing the amount of carbon assimilated per leaf and gross photosynthesis as a result of fertilization. Plants might just be allocating more of the available nutrients to woody biomass rather than to enhancing their leaves. Our woody and

foliar estimates might not accurately portray the changes in woody or foliar biomass. The estimates do not take into account changes in mass or thickness of the woody material. The estimates provide a total volume of the woody or foliar material and might not accurately represent changes in woody or foliar biomass with nutrient addition. Alternatively, some factor could be inhibiting the function of rubisco. Further investigation is necessary in order to understand the changes in woody and foliar biomass, and the possible limitation of other nutrient.

The increase in LAI (Leaf Area Index) could be attributed to a denser canopy resulting from the increase in leaves and also the increase in plant woody material allowing each plant to grow more spread out and effectively shade more light. The increase in LAI suggests that there is increased shading due to the growth of vascular plants and the shading could cause a decline n *Sphagnum.* The shift in the C: N ratio with nutrient addition suggests that plants are incorporating some of the fertilizer and that the nutrients are not just immobilized by microbes. The increase in leaf litter may be a result of increasing leaf number and may lead to an increase in biomass turnover with the addition of (limiting) nutrients. Litter build up and changes in litter composition affect decomposition rates and the system's ability to store carbon.

Overall, the plants are taking up less carbon but increasing biomass. The increase in litter production might also increase the loss of carbon from the system. These results have important implications for the future of carbon storage within Mer Bleue and peatland systems as environmental change increases.

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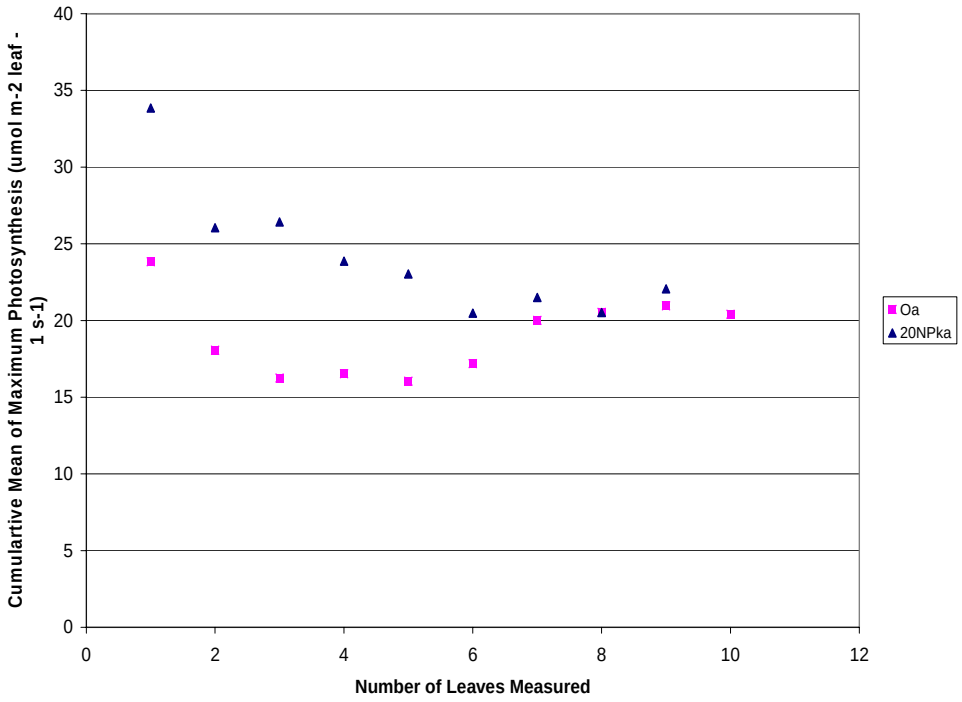

Figure 1: Cumulative mean of maximum photosynthetic rate for *Chamaedaphne* light curve data

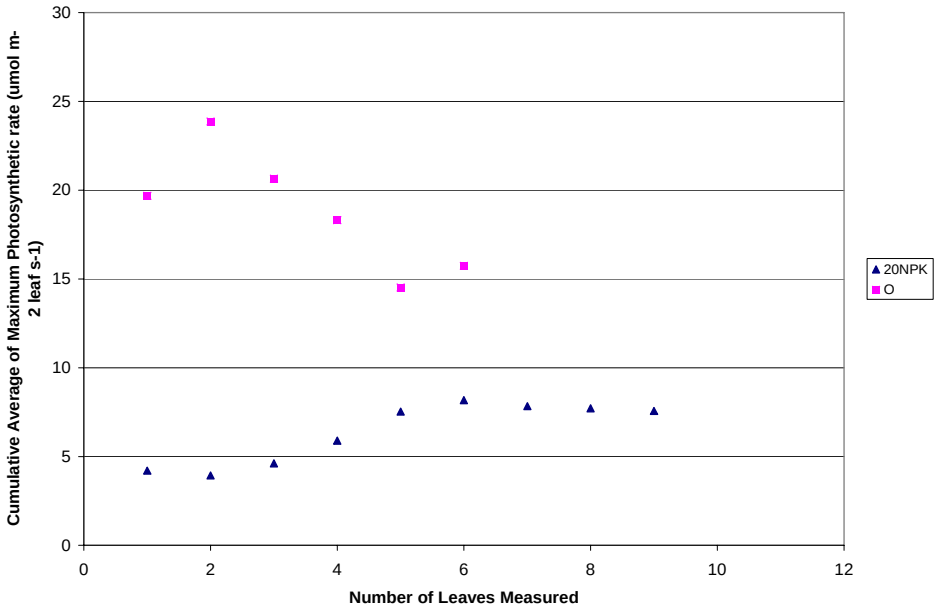

Figure 2: Cumulative mean of maximum photosynthetic rate for *Ledum* light curve data

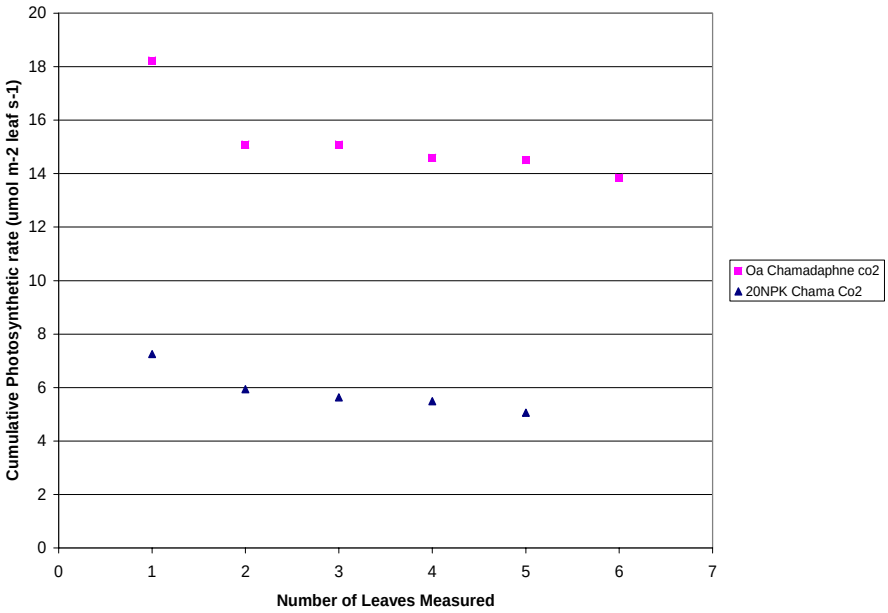

Figure 3: Cumulative mean graph of maximum photosynthesis rate for *Chamaedaphne* based on CO2 response curve data

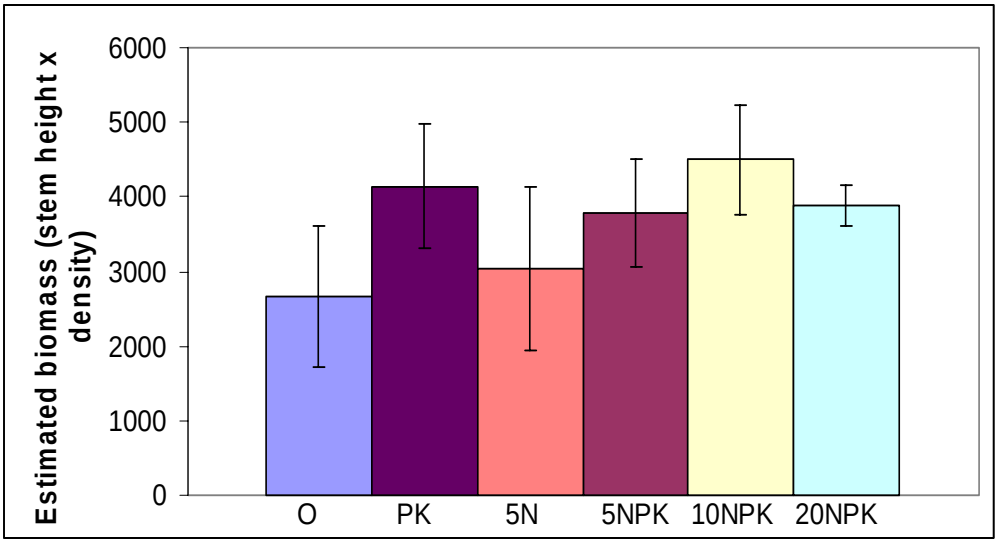

Figure 4: Estimated biomass for all treatments. Shows no significant difference

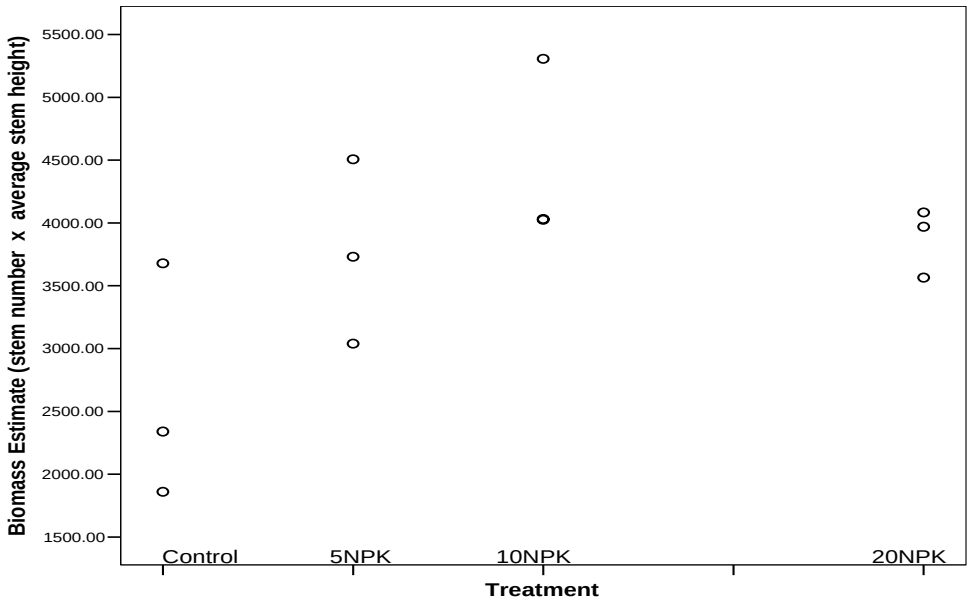

Figure 5: Estimated biomass for NPK and control plots

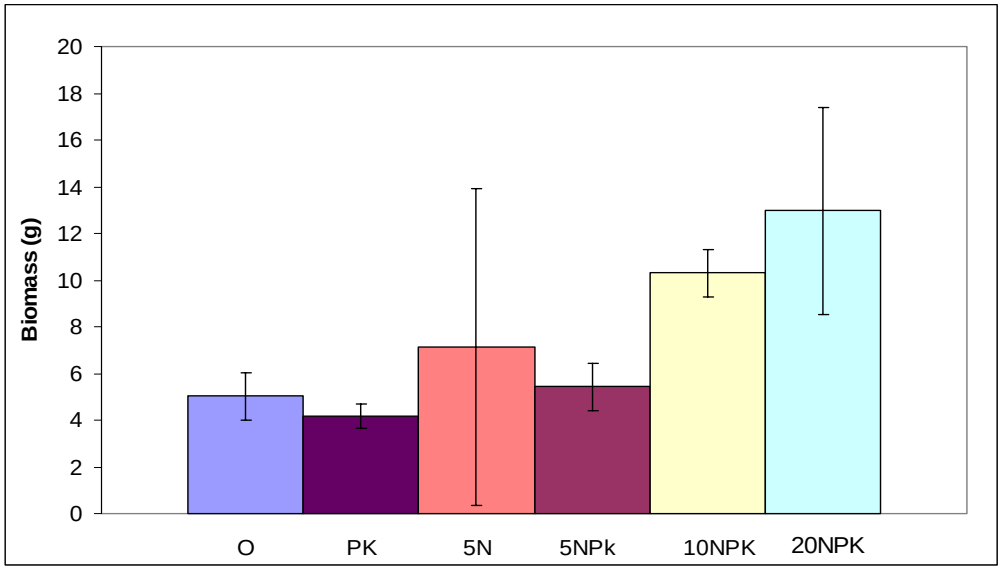

Figure 6: Measured biomass from the clipped plant samples (marginally significant relationship)

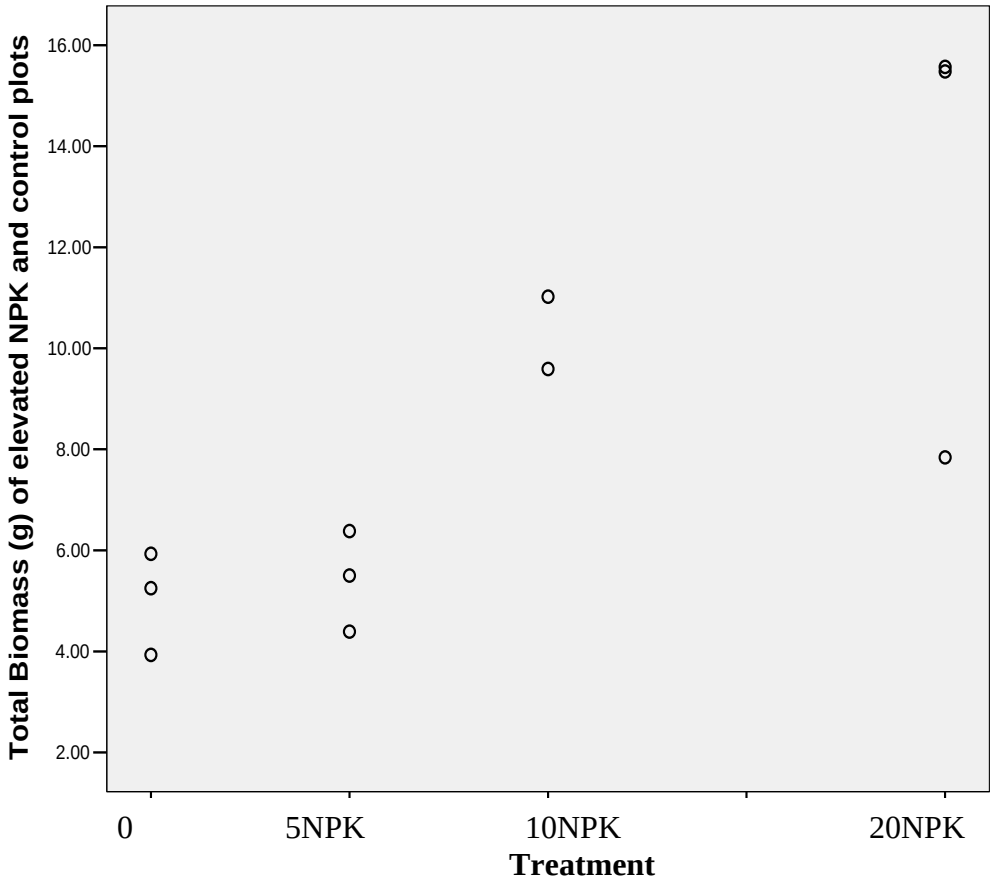

Figure 7: Total biomass for the elevated NPK and control treatments

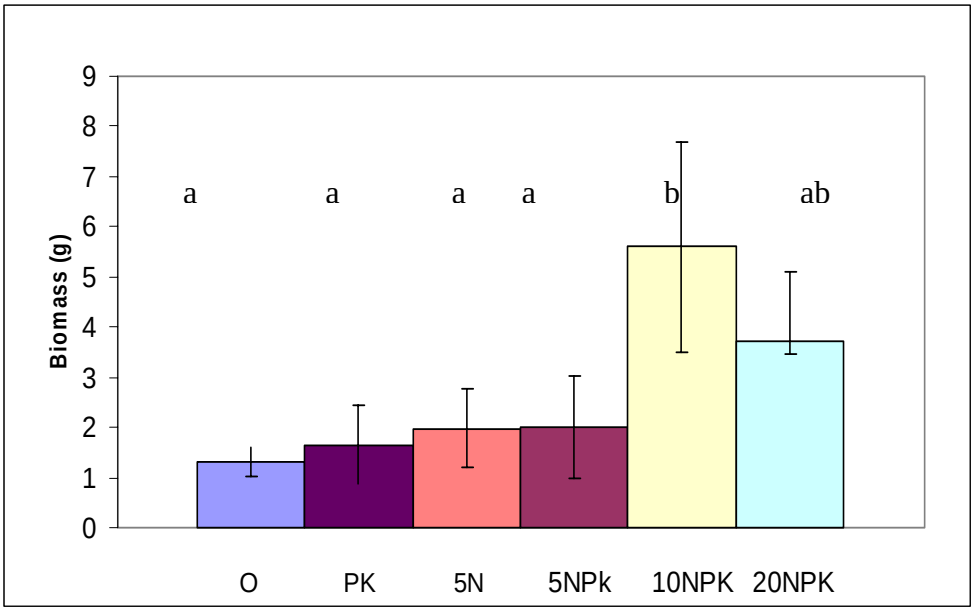

Figure 8: *Chamaedaphne* Biomass

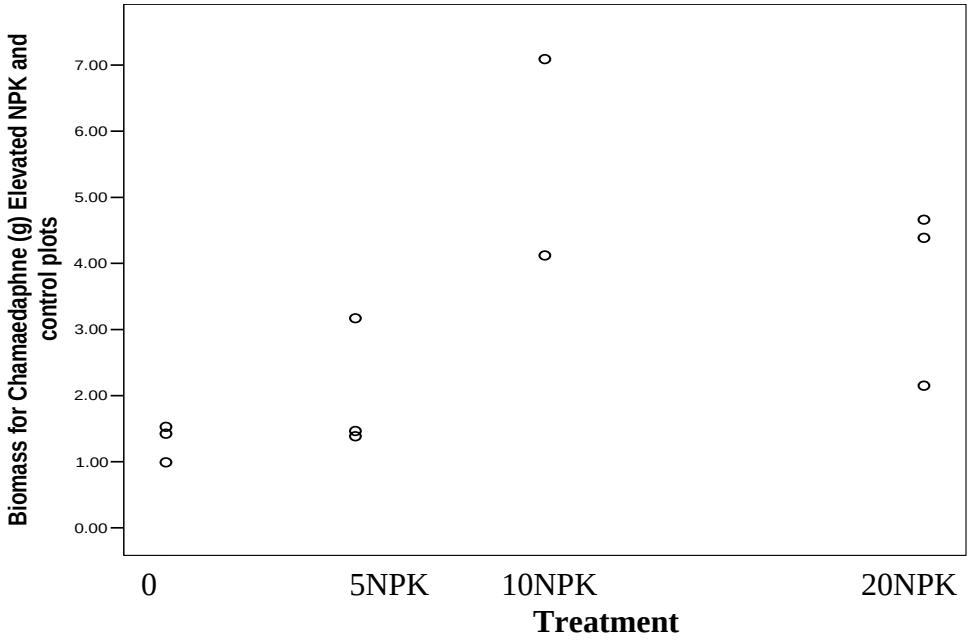

Figure 9: *Chamaedaphne* Biomass for the elevated NPK and control plots

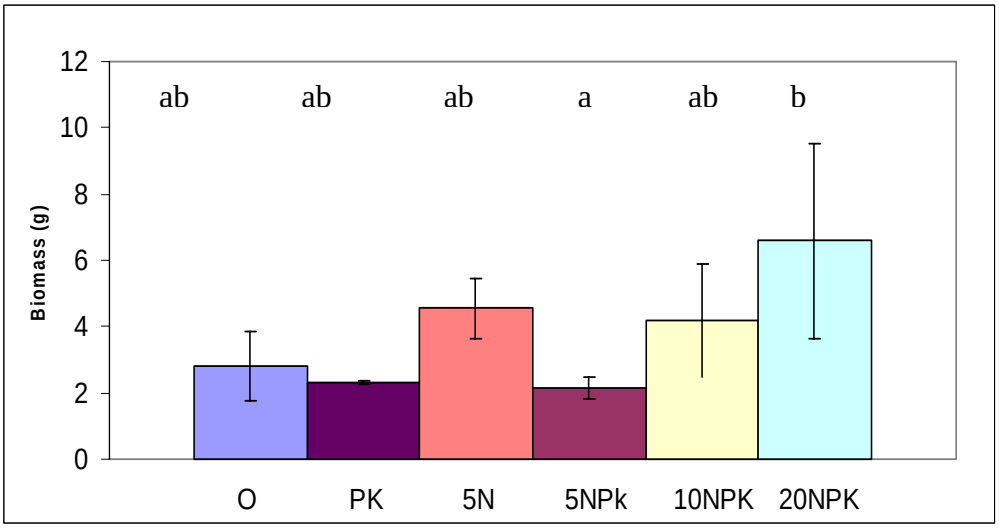

Figure 10: *Ledum* Biomass

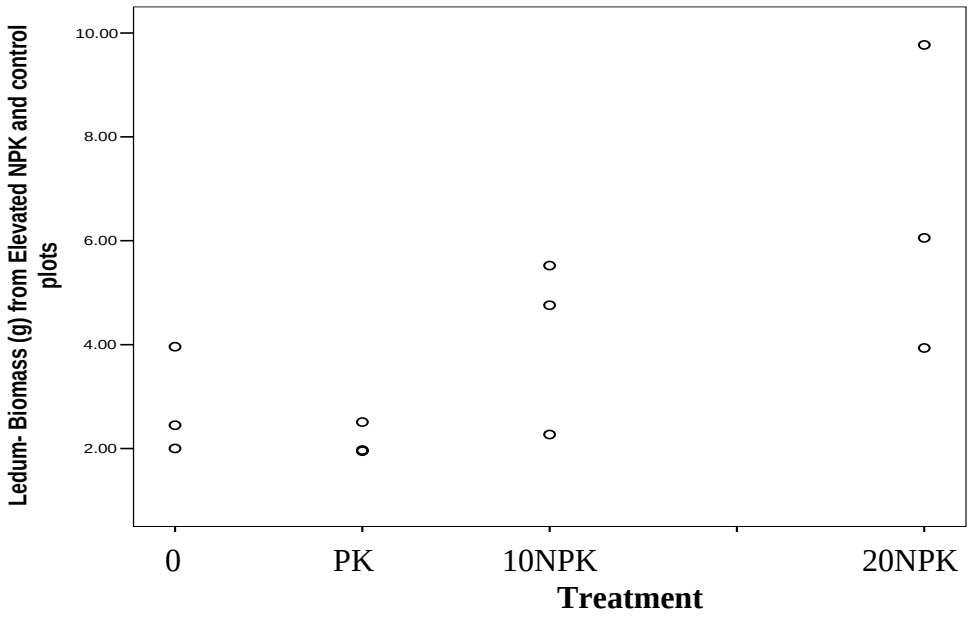

Figure 11: *Ledum* Biomass used in regression (elevates NPK and control plots)

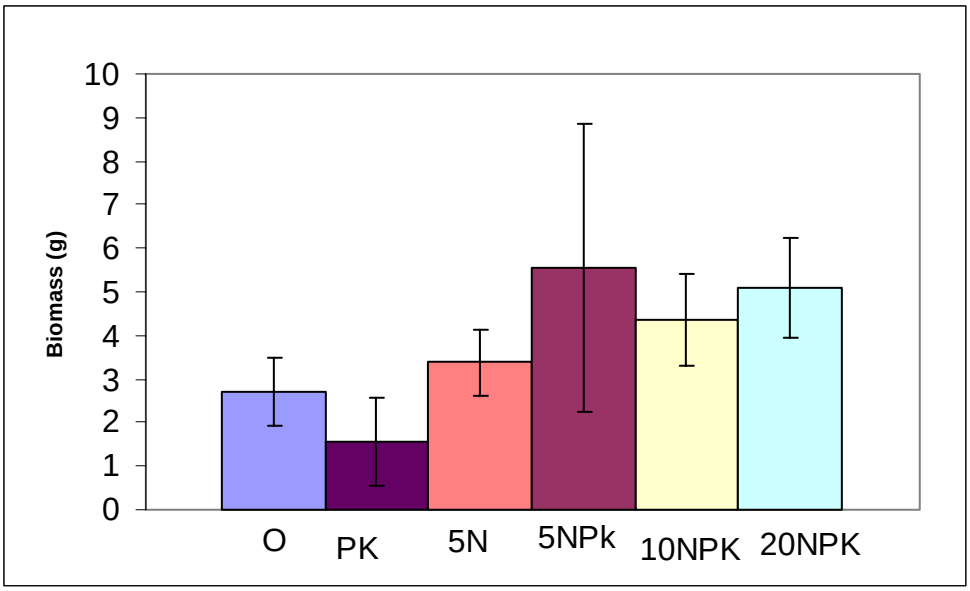

Figure 12: *Vaccinium* Biomass. Shows no significant difference

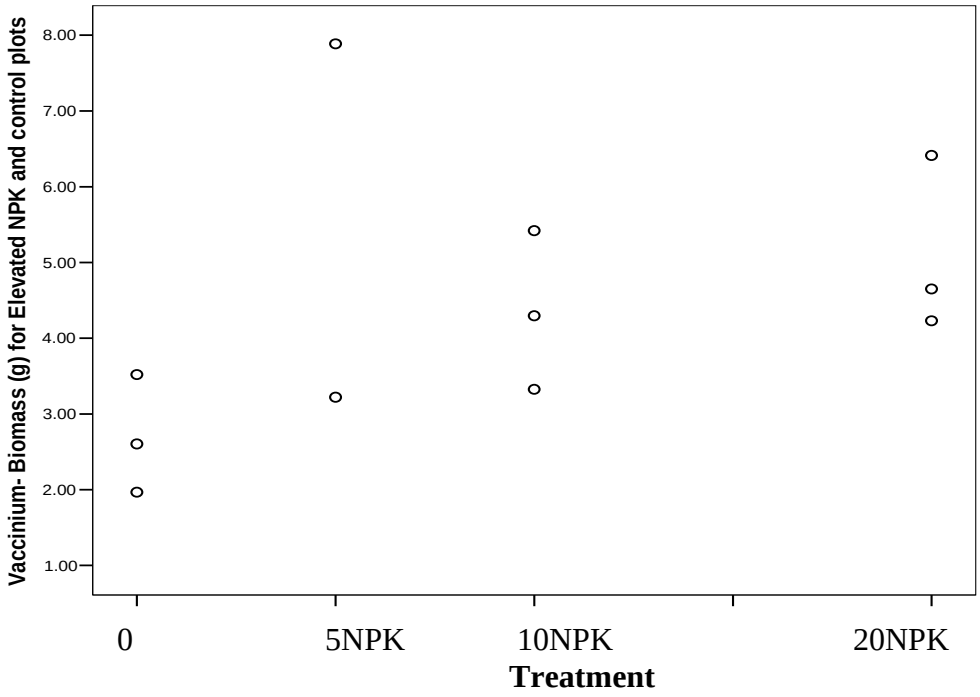

Figure 13: *Vaccinium* biomass used in regression (elevated NPK and control plots)

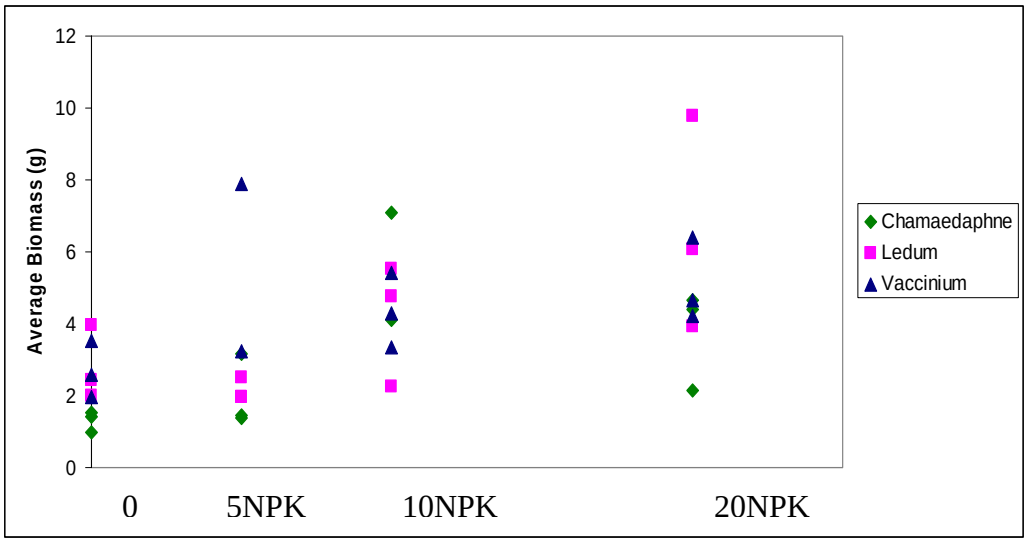

Figure 14: Mass of three species for elevated NPK and control plots

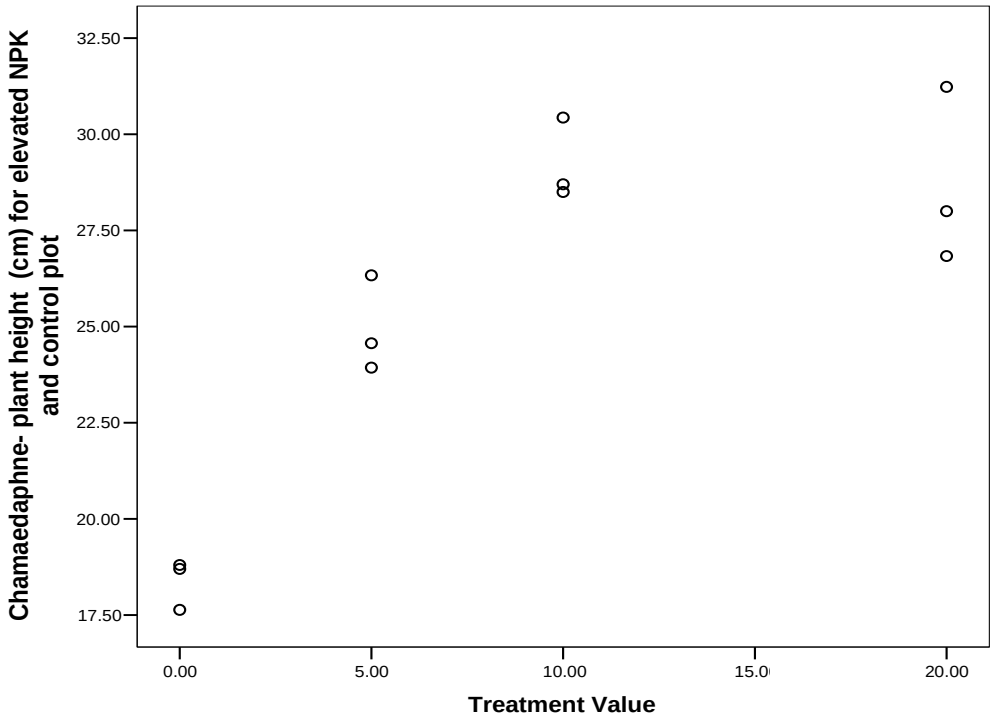

Figure 15: Plant height for *Chamaedaphne*

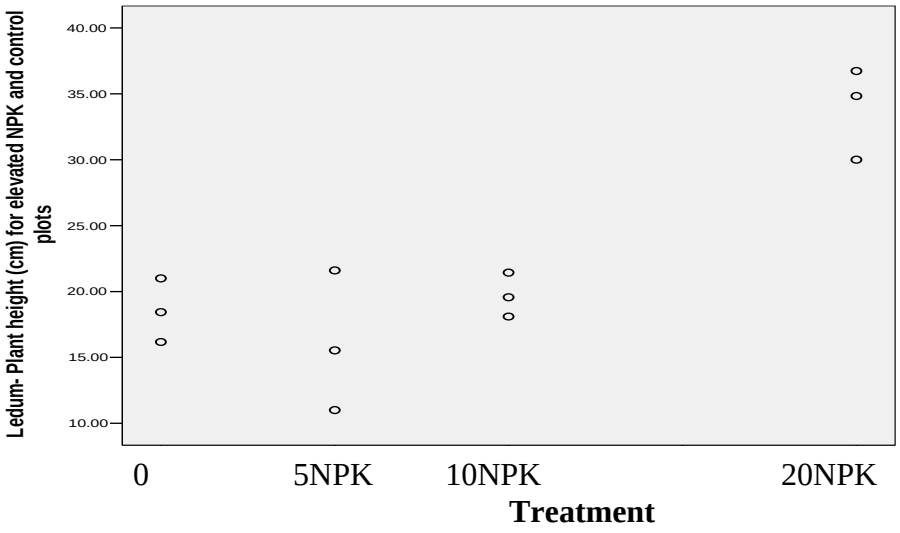

Figure 16: Plant height for *Ledum*

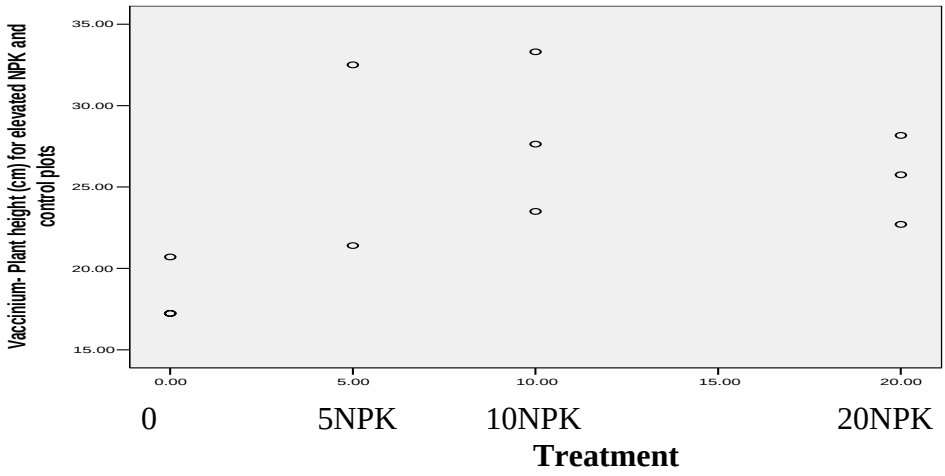

Figure 17: Plant height for *Vaccinium*

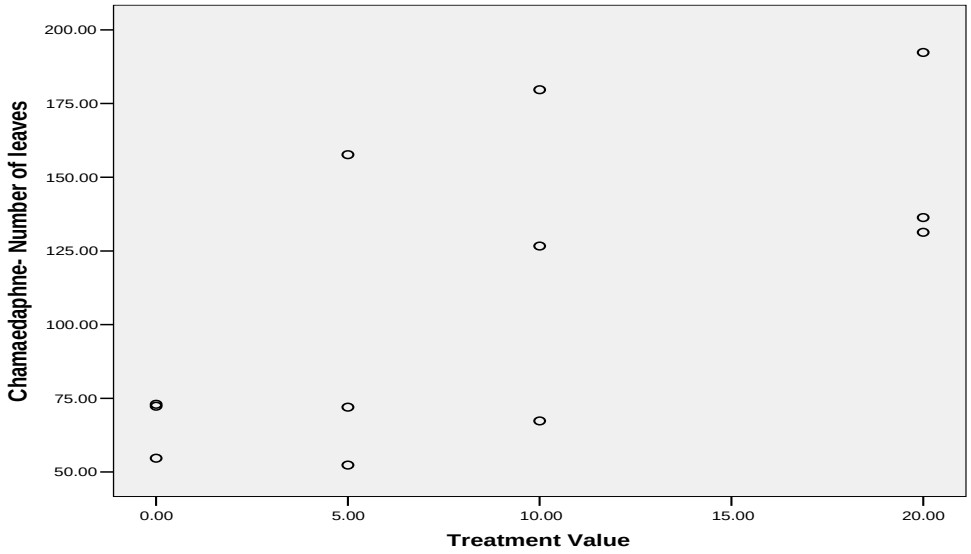

Figure 18: Number of leaves for *Chamaedaphne* within the elevated NPK and control plots

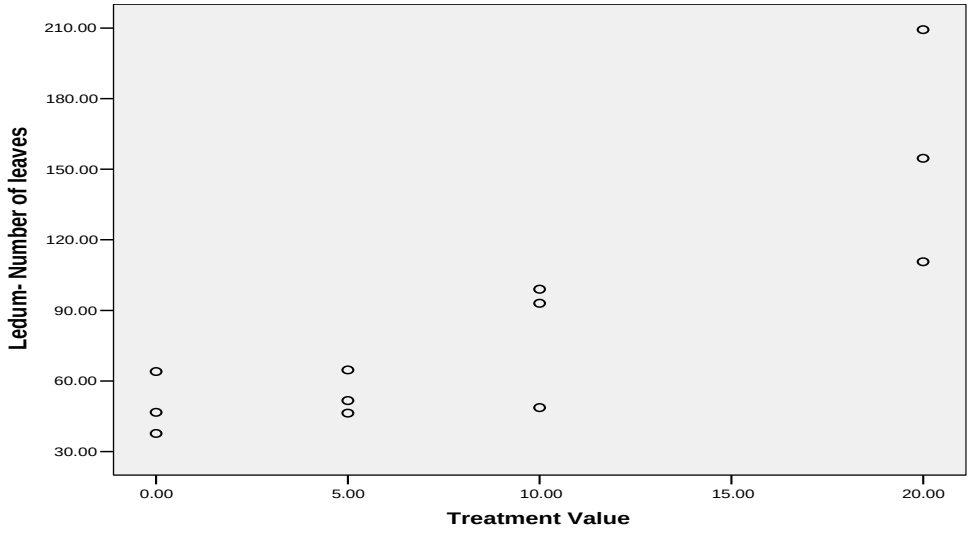

Figure 19: Number of leaves for *Ledum* within the elevated NPK and control plots

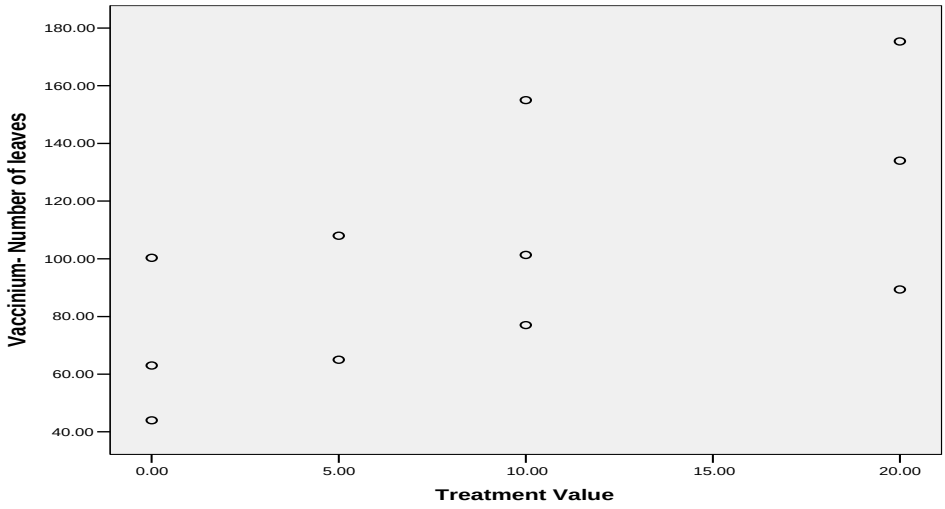

Figure 20: Number of leaves for *Vaccinium* within the elevated NPK and control plots

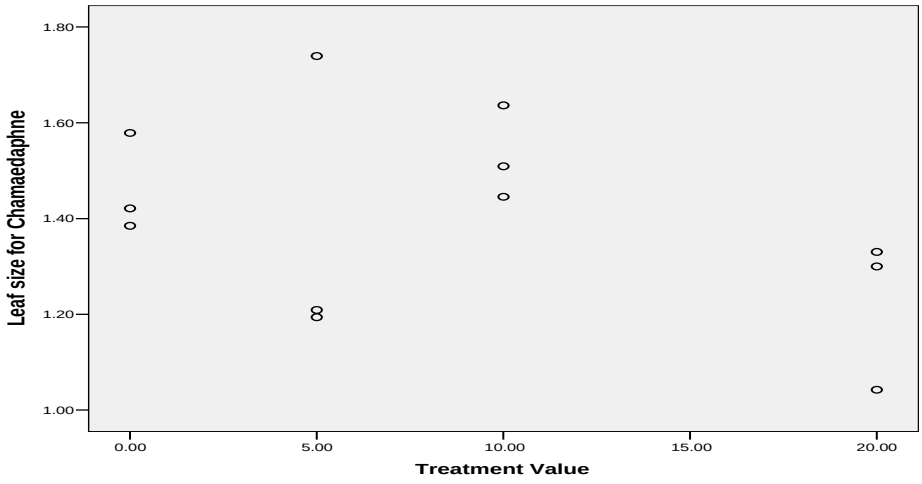

Figure 21: Leaf size for *Chamaedaphne* within the elevated NPK and control plots

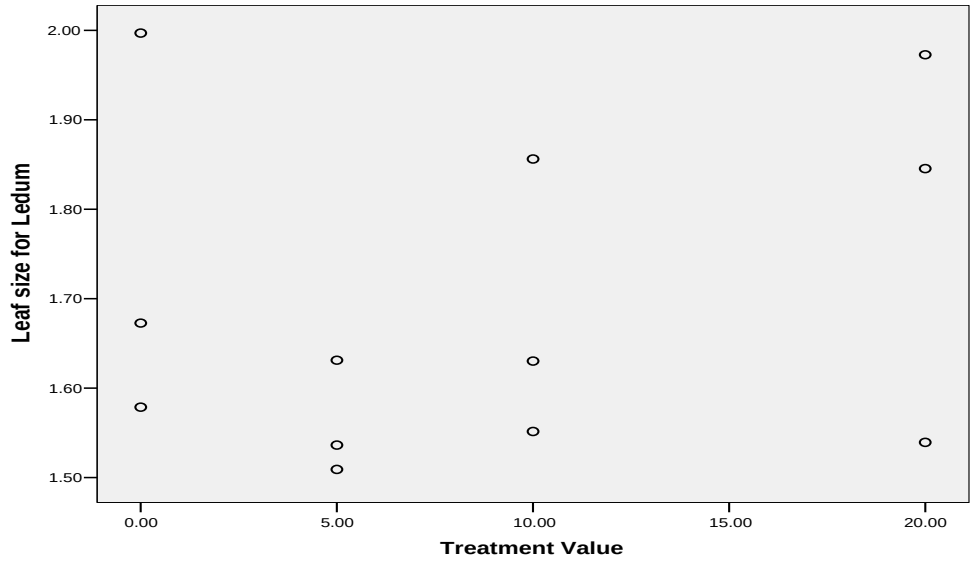

Figure 22: Leaf size for *Ledum* within the elevated NPK and control plots

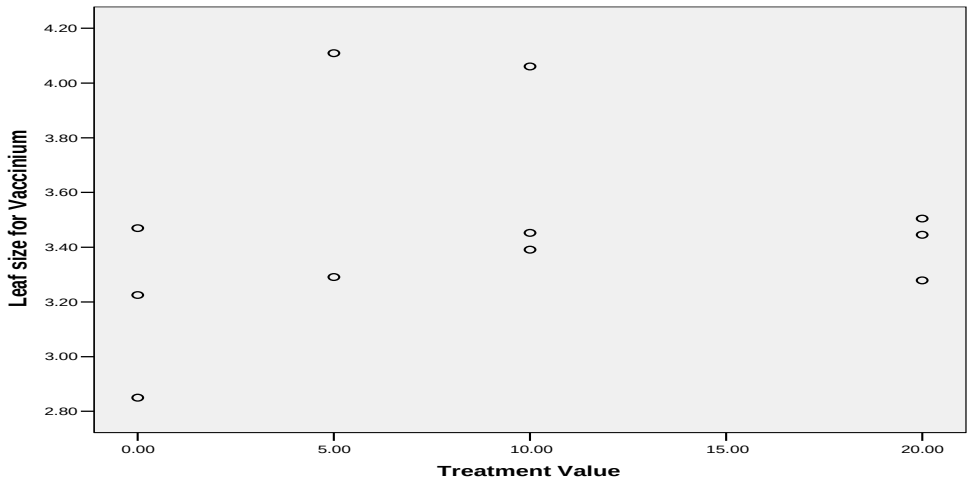

Figure 23: Leaf size for *Vaccinium* within the elevated NPK and control plots

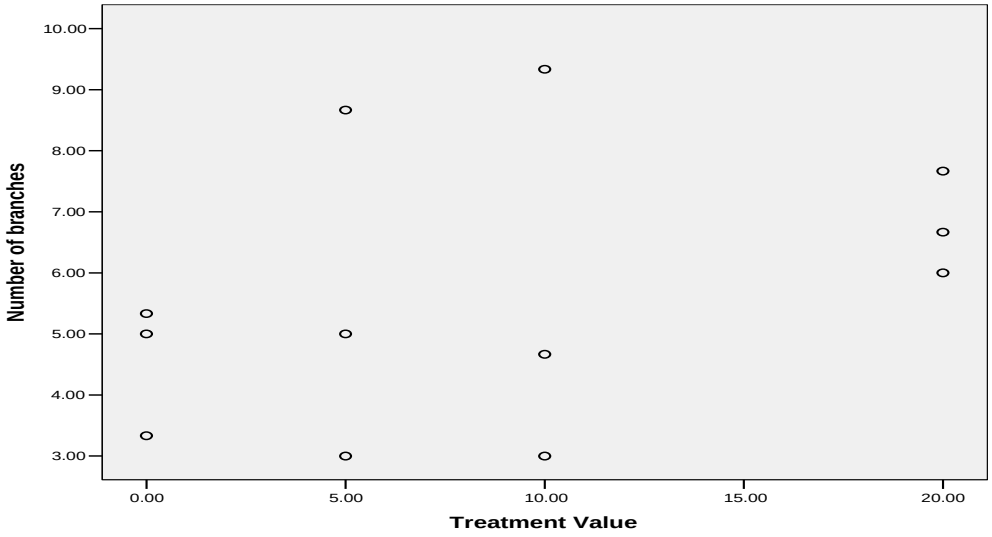

Figure 24: Number of branches for *Chamaedaphne* from elevated NPK and control plots

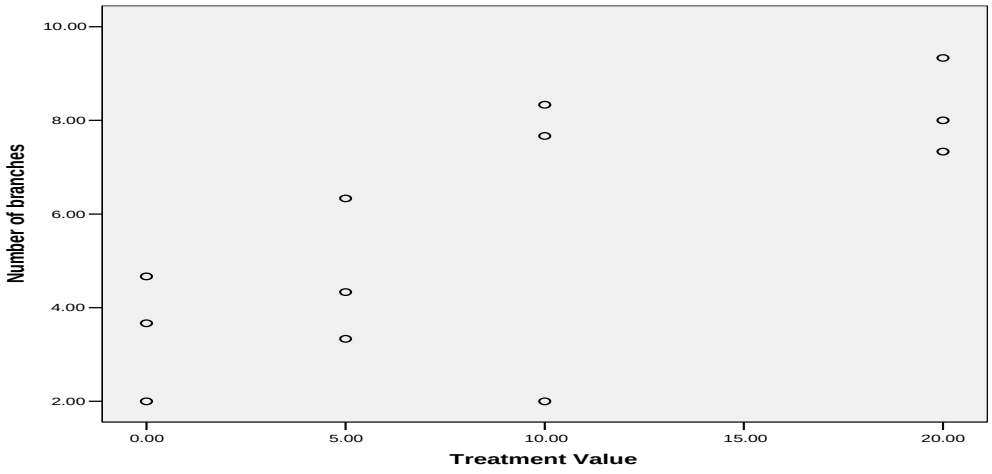

Figure 25: Number of branches for *Ledum* from elevated NPK and control plots

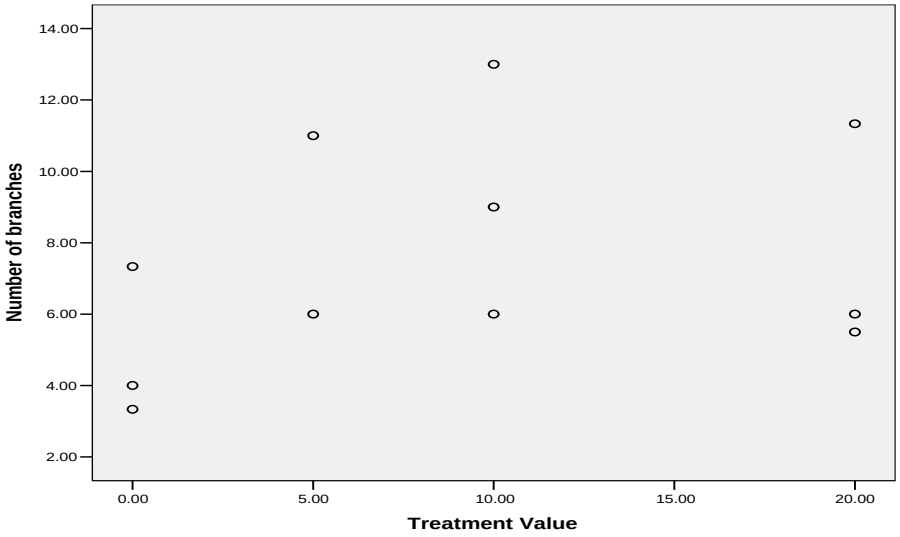

Figure 26: Number of branches for *Vaccinium*

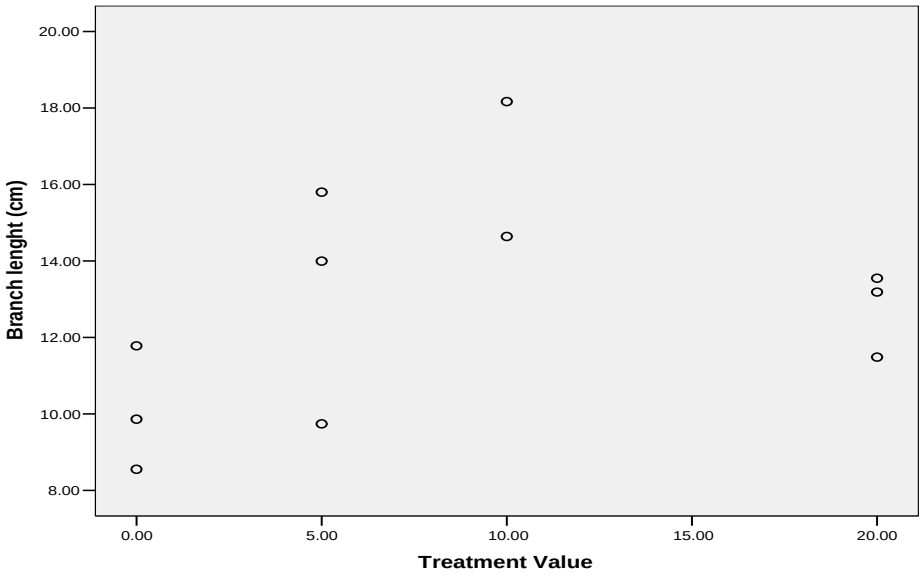

Figure 27: Branch Length for *Chamadaphne*

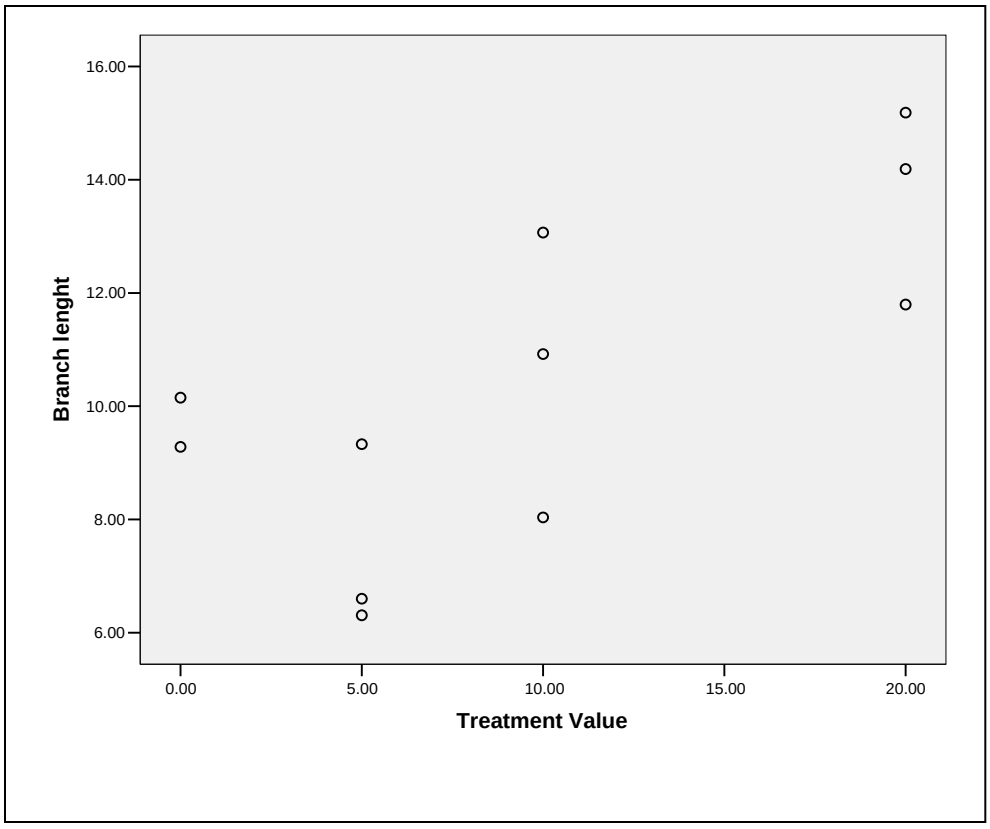

Figure 28: Branch length for *Ledum*

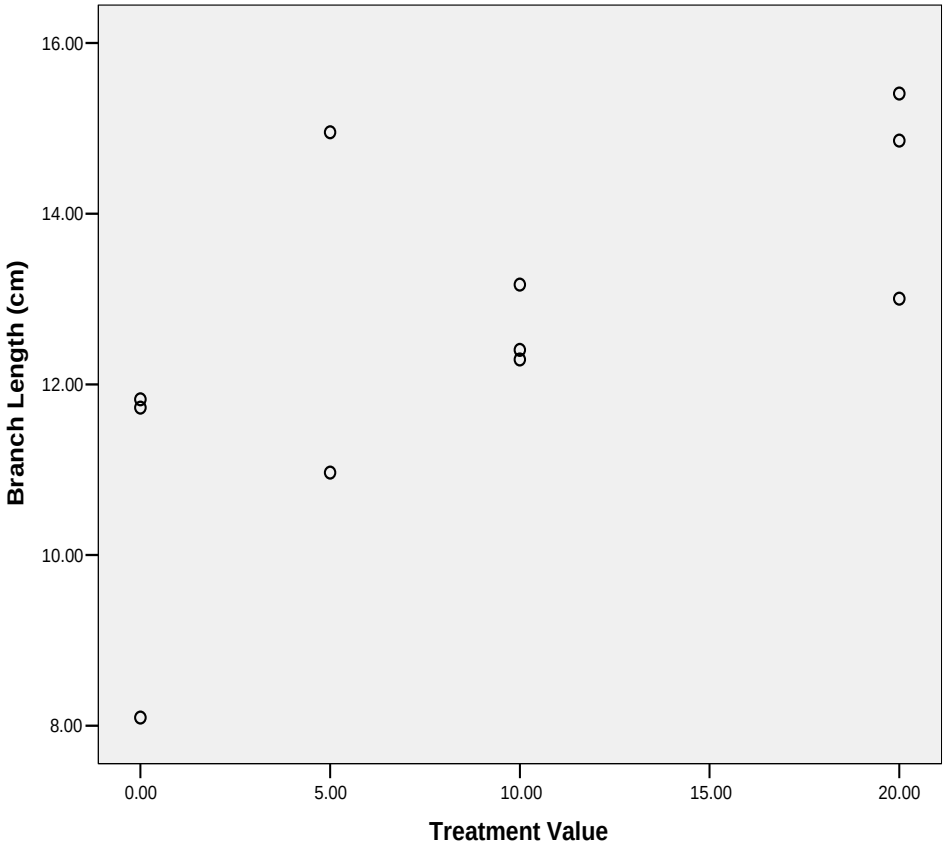

Figure 29: Branch length for *Vaccinium*

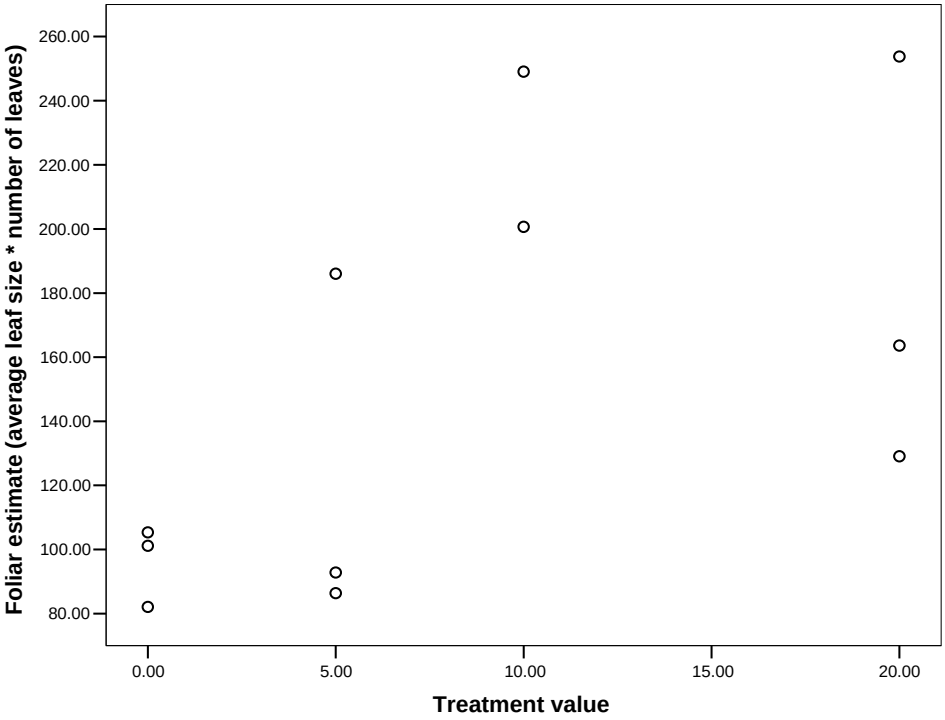

Figure 30: Foliar estimate for *Chamaedaphne*

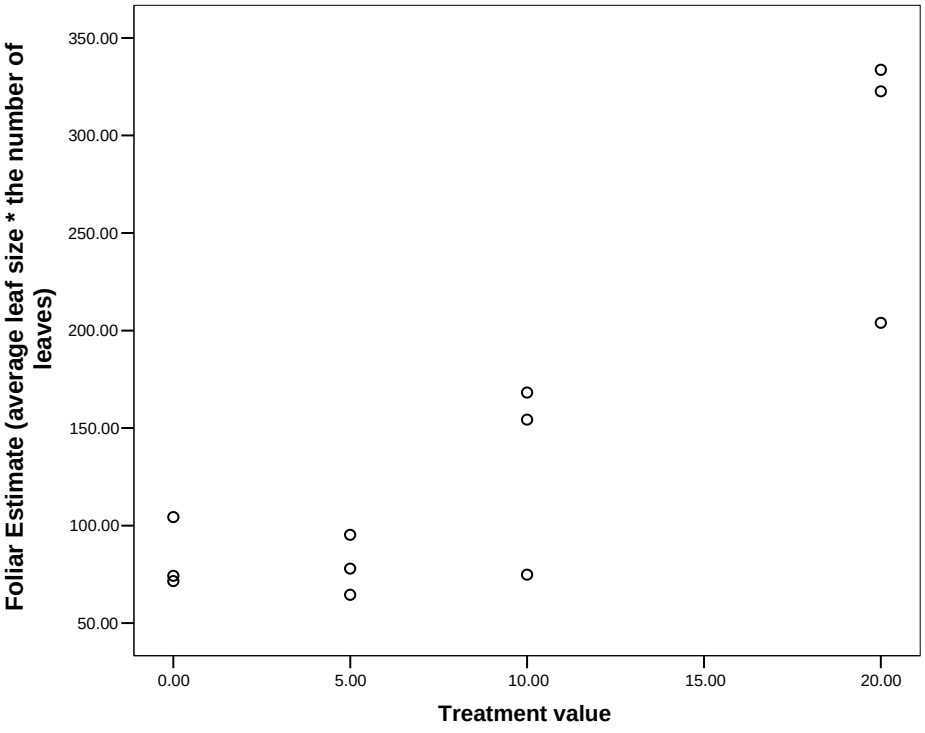

Figure 31: Foliar Estimate for *Ledum*

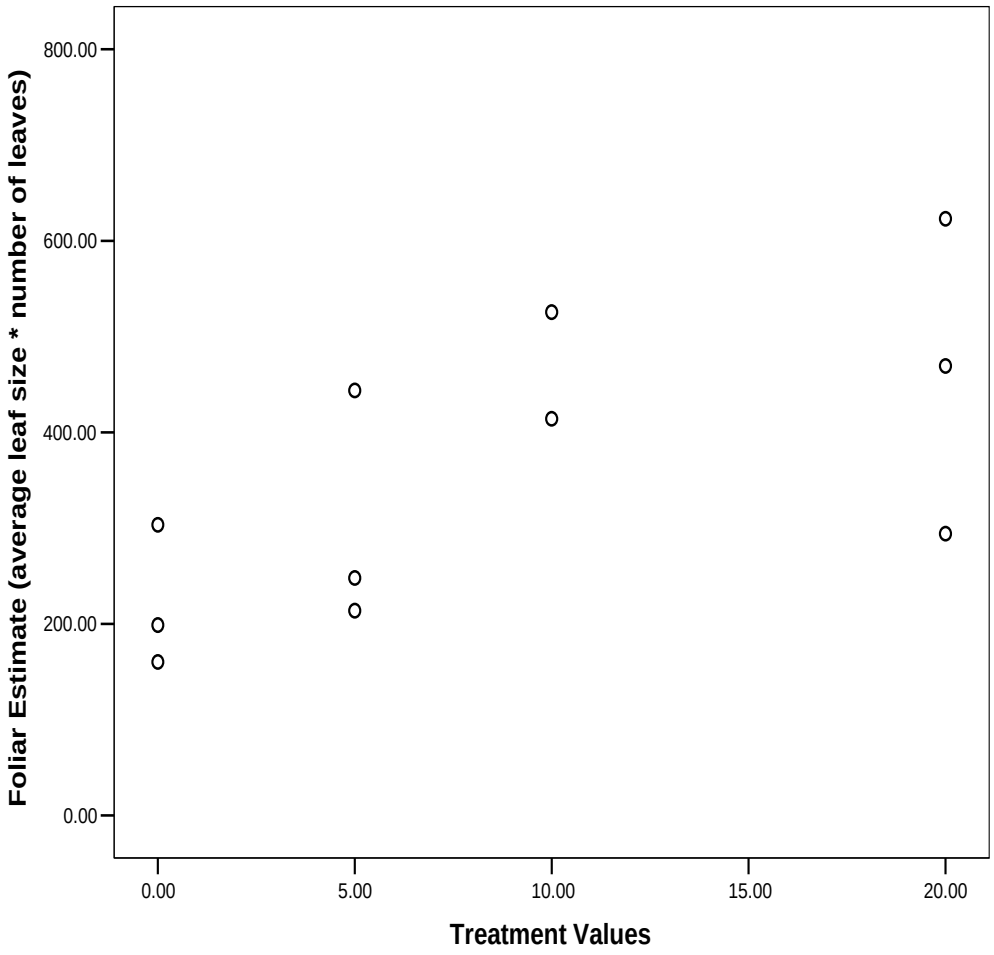

Figure 32: Foliar Estimate for Vaccinium

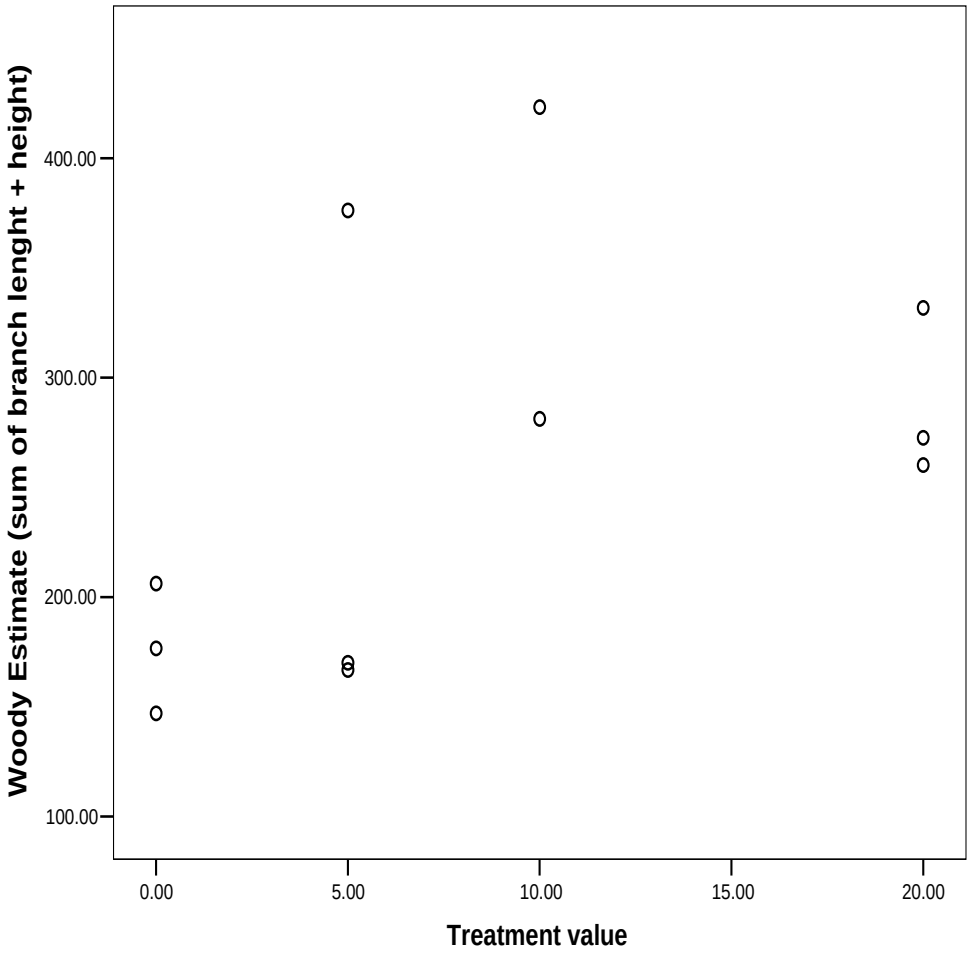

Figure 33: Woody estimate for *Chamaedaphne*

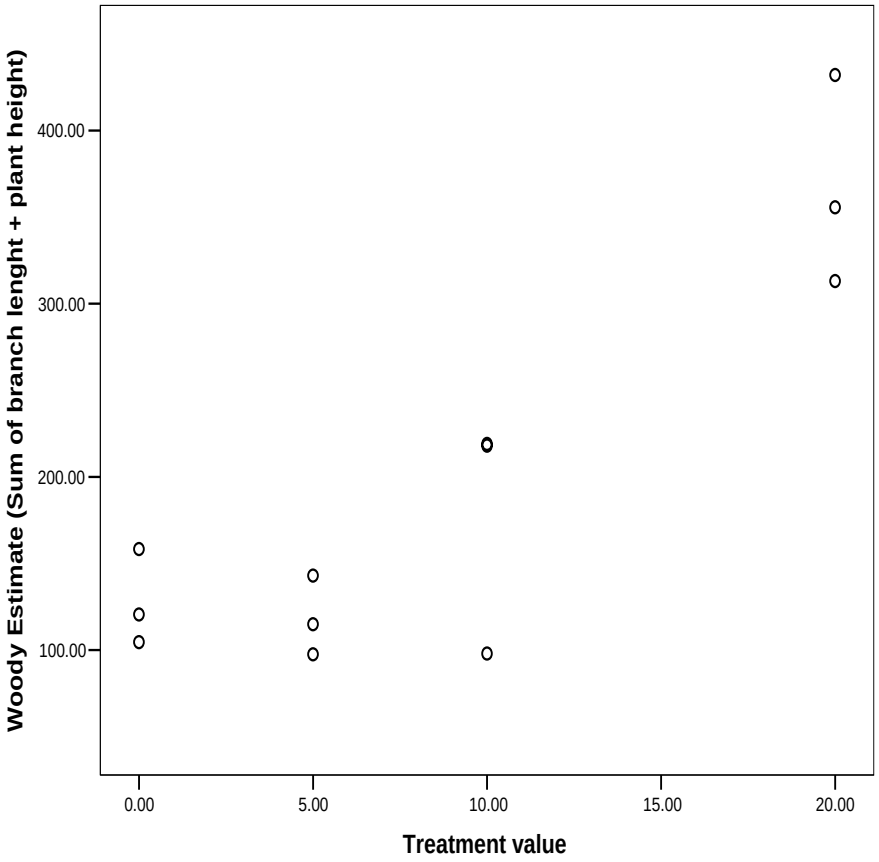

Figure 34: Woody estimate for Ledum

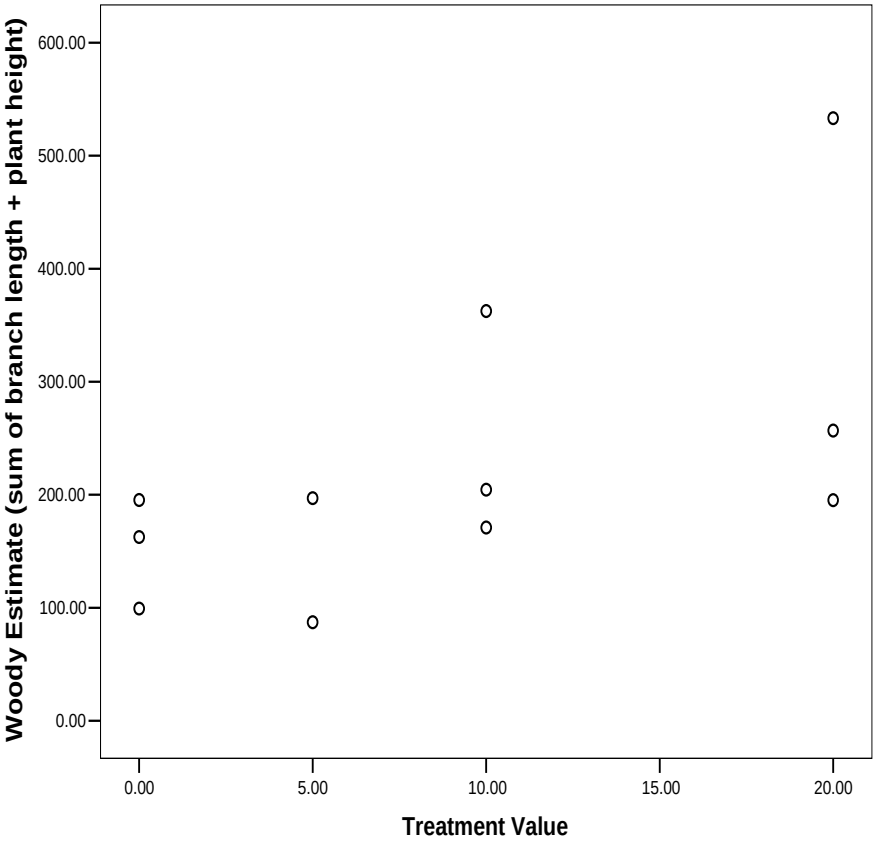

Figure 35: Woody estimate for *Vaccinium*

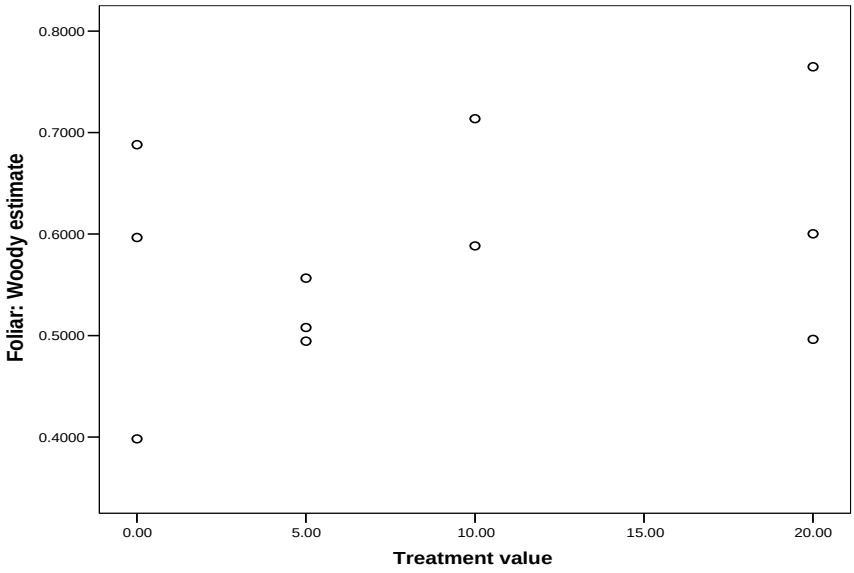

Figure 36: Foliar: Woody ratio for *Chamaedaphne*

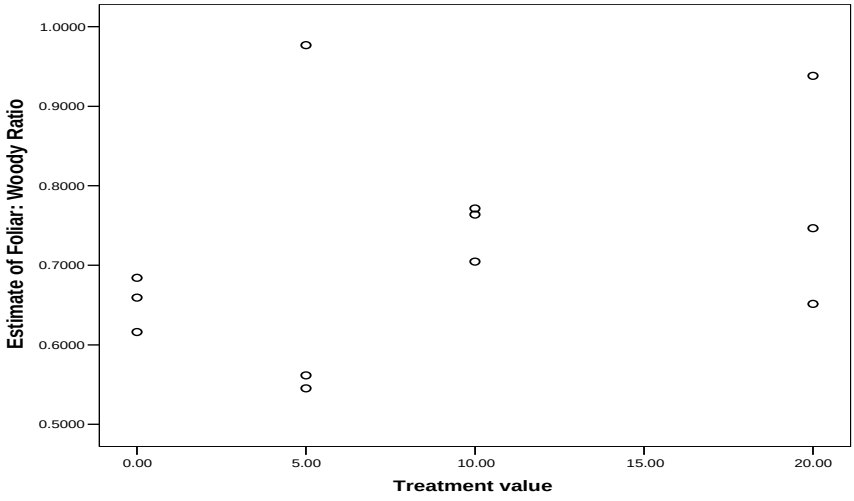

Figure 37: Estimate of Foliar: Woody for *Ledum*

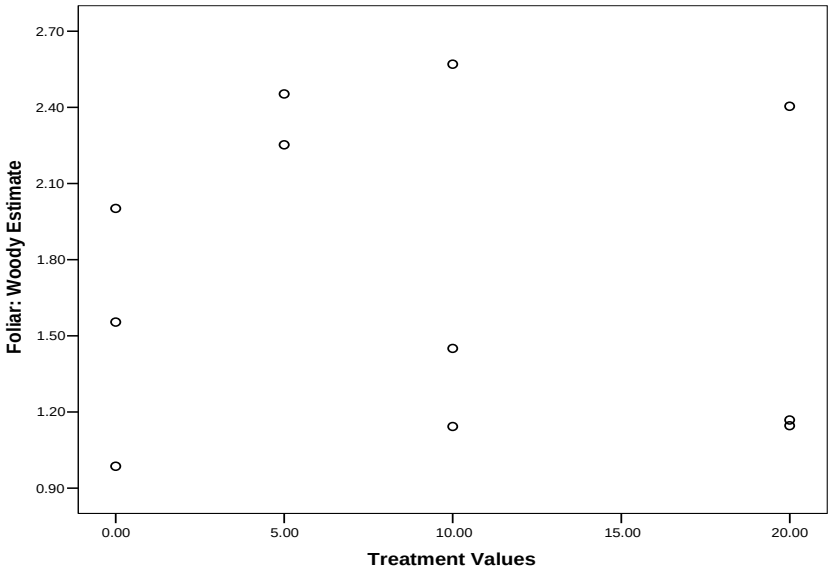

Figure 38: Foliar: Woody estimate for *Vaccinium*

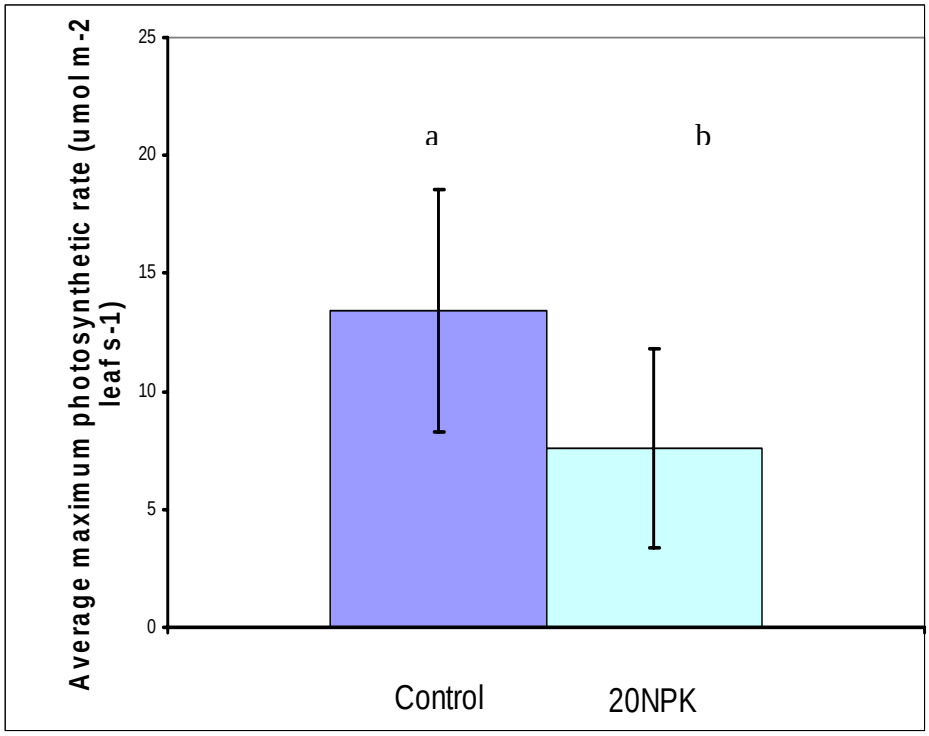

Figure 39: Maximum photosynthetic rate for *Ledum* using the response curve data

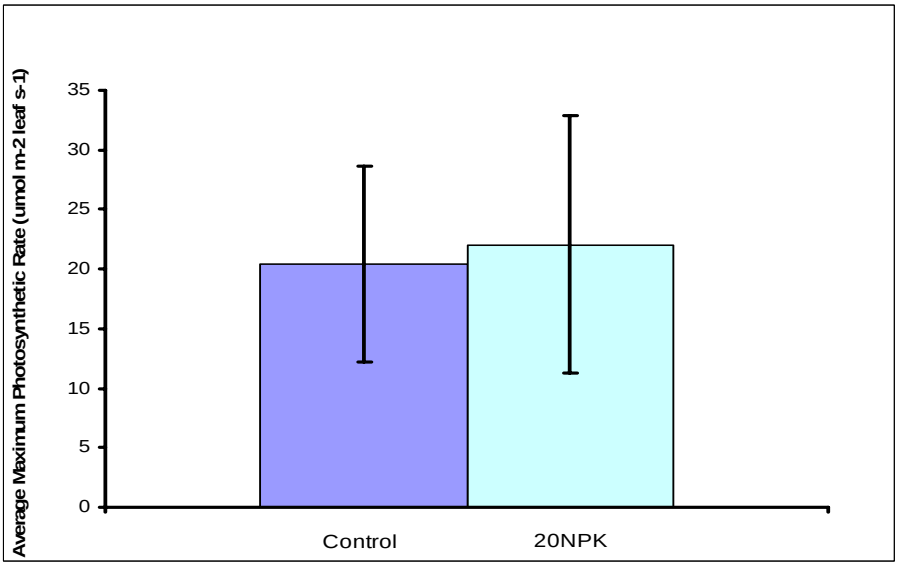

Figure 40: Maximum photosynthetic rate for *Chamaedaphne* using the light response curve data

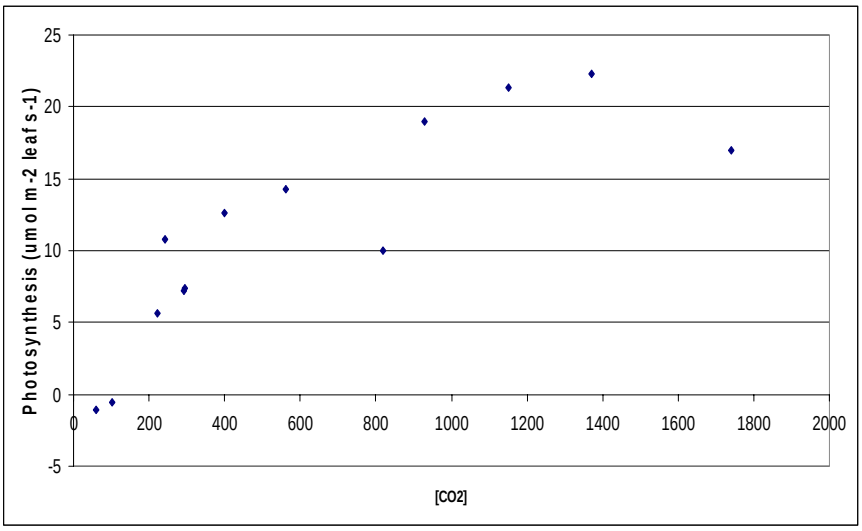

Figure 41: CO_2 response curve for *C. calyculata* measured in a control plot

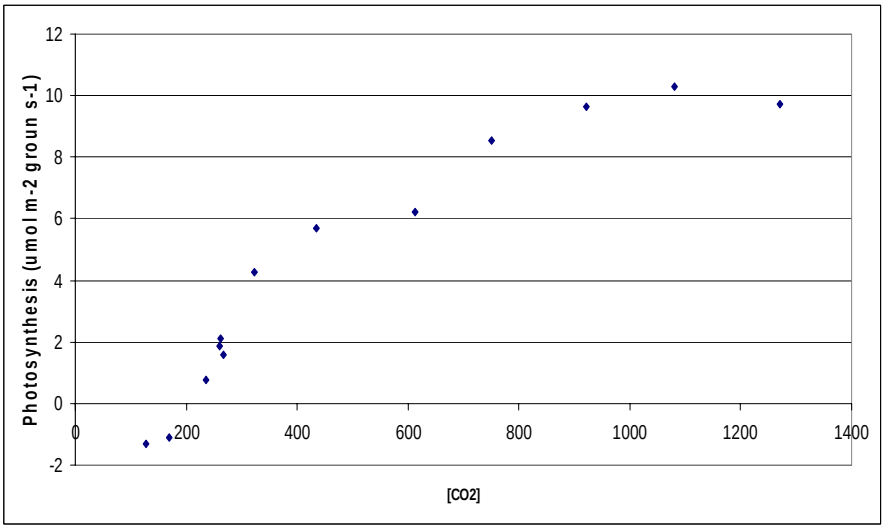

Figure 42: CO_2 response curve for *L. groenlandicum* measured in a control plot

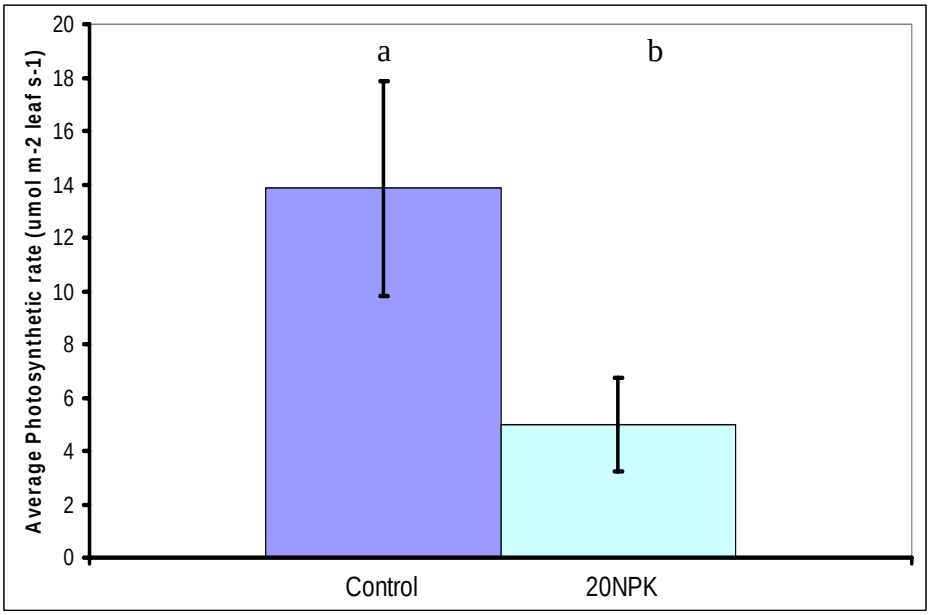

Figure 43: Maximum photosynthetic rate for *Chamaedaphne* using the CO2 response curve data

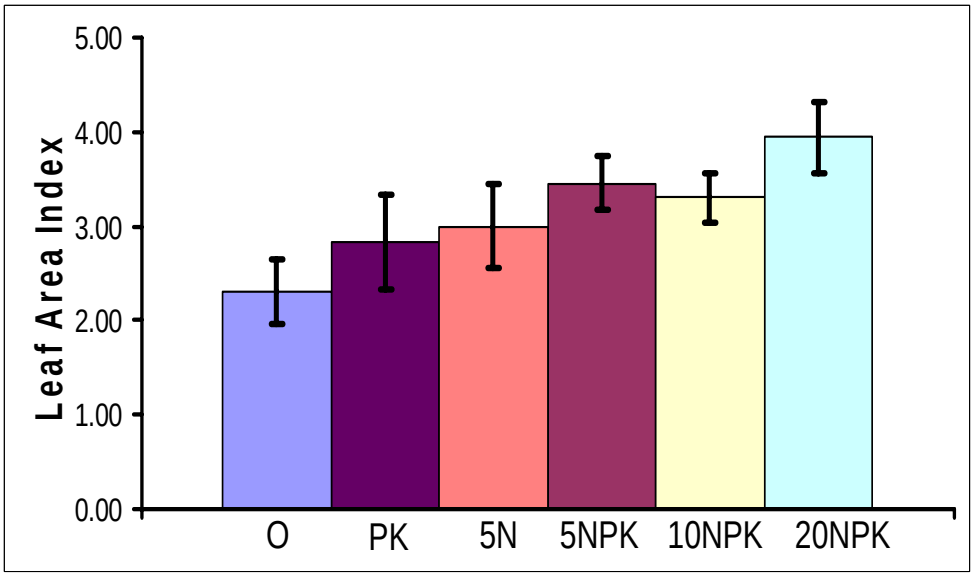

Figure 44: LAI for all plots

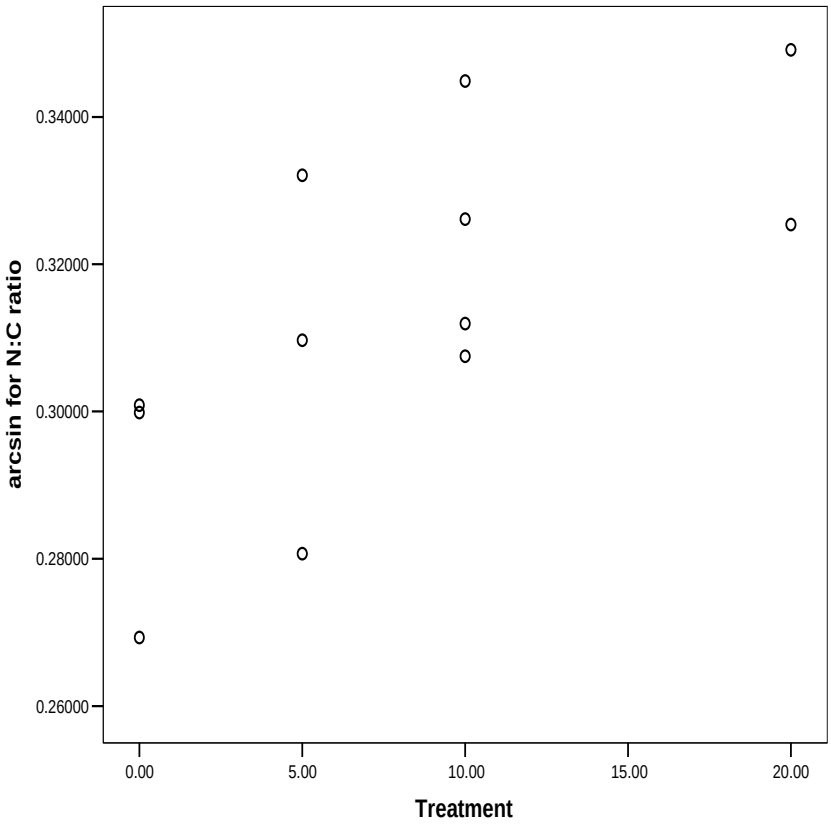

Figure 45: C: N ratio for *Chamaedaphne*

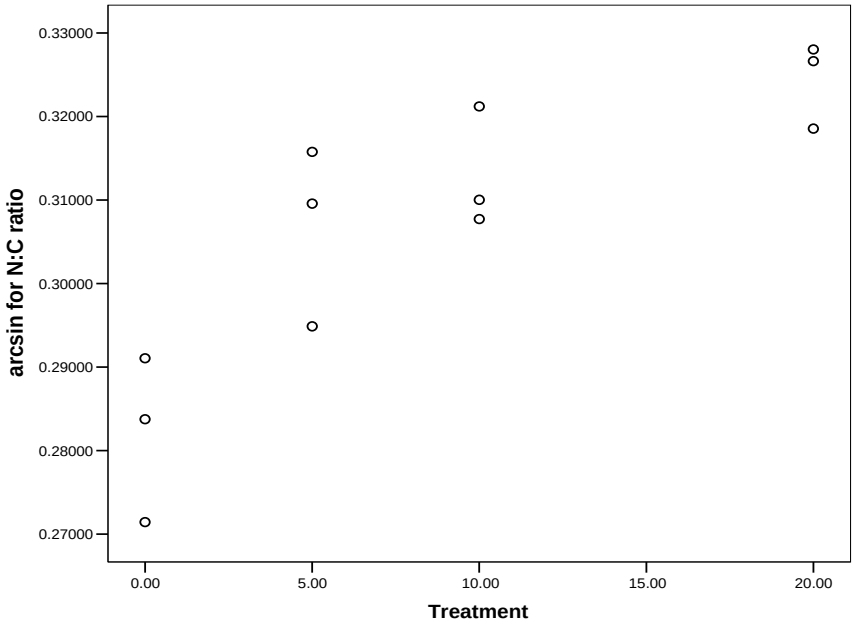

Figure 46: C: N ratio for *Ledum*

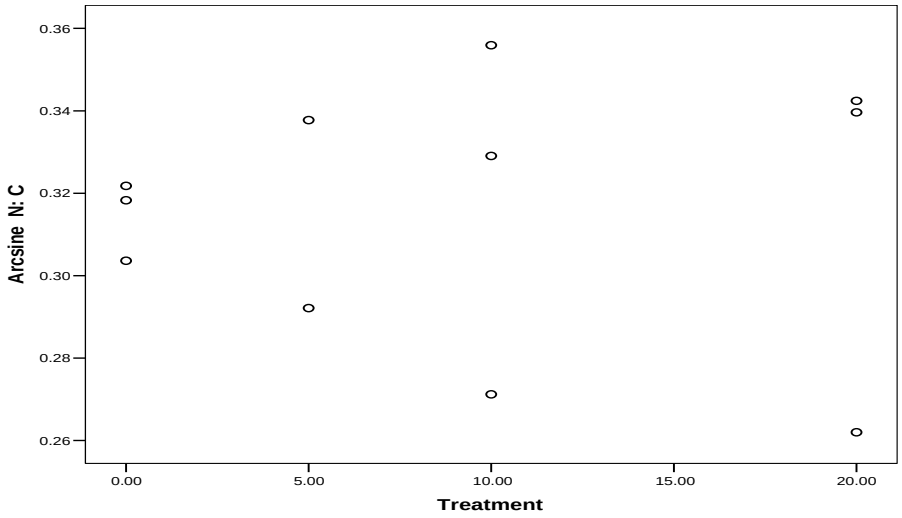

Figure 47: N: C ratio for *Vaccinium*

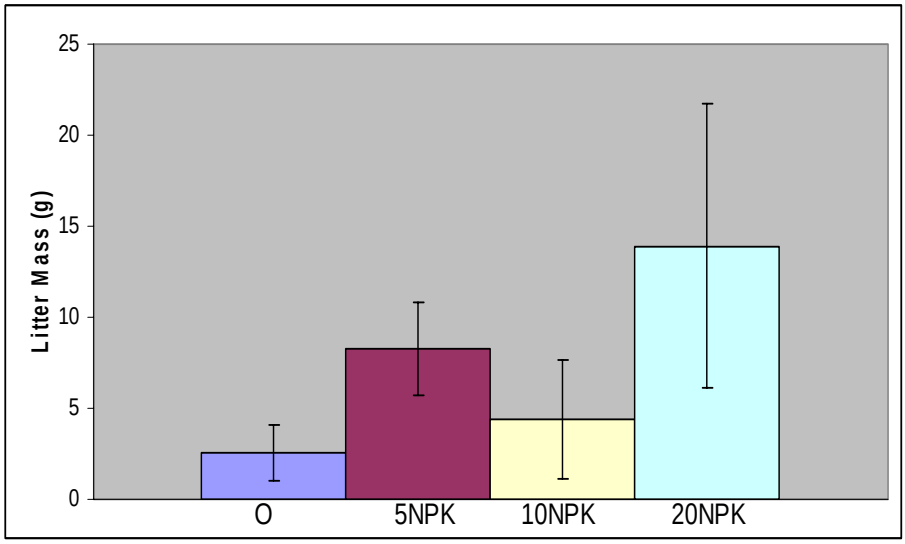

Figure 48: Average litter mass for elevated NPK and control plots

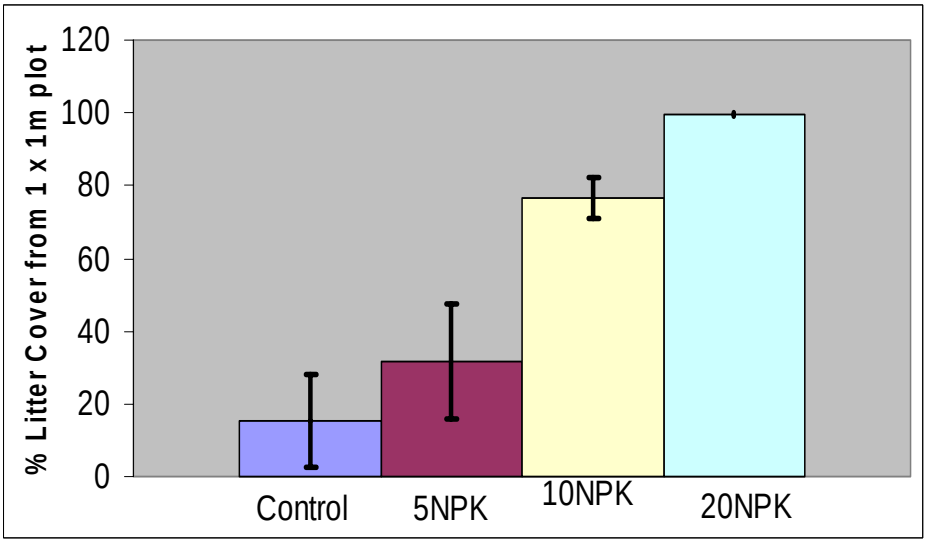

Figure 49: Percent litter cover from with in 1 x 1m collar

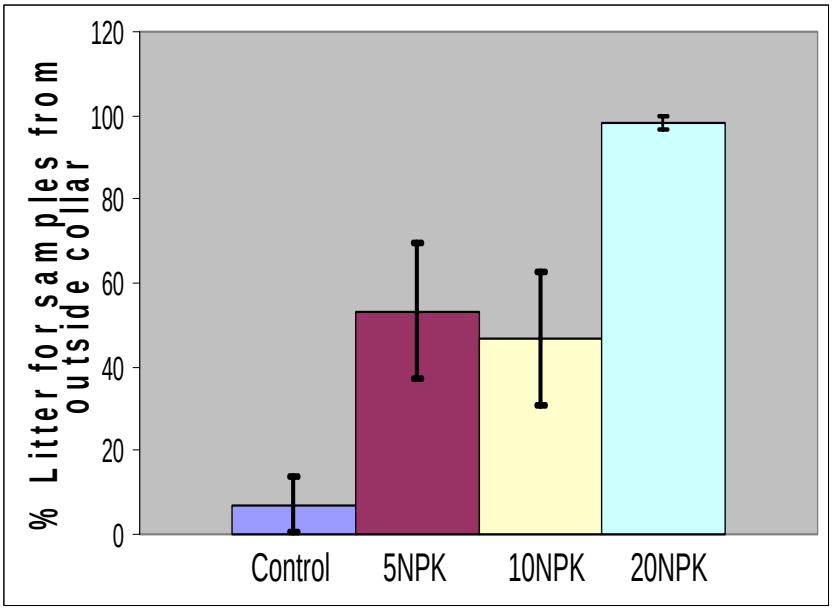

Figure 50: Percent litter cover from outside of the 1x1m collar

Table 1: Summary of statistical analysis for stem height x density data- See figures

Comparison	**Analysis**	**F or T- stat**	**df (numerator, denominator)**	**r2**	**P-value**
All 6 treatments	One- Way ANOVA	2.17	5, 12		0.125
Elevated NPK and control (5NPK, 10NPK, and 20NPK)	Regression	3.147		0.56	0.025

Table 2: Summary of estimated biomass data

Plot	**Average**	**Standard Deviation**
20NPK	3884.04	264.96
10NPK	4495.97	734.14
5NPK	3785.38	719.38
5N	3038.10	1097.89
PK	4137.76	830.08
Control	2668.19	944.85

Table 3: Summary of statistical analysis for biomass data

Comparison	**Analysis**	**T-stat or F**	**df (numerator, denominator)**	**R 2**	**P-value**
Total Biomass	One-Way ANOVA	2.91	5, 12		0.06
Control and Elevated NPK	Regression	2.42	10	0.371	0.036
C. calyculata	One- Way ANOVA	4.99	5, 12		0.011
C. calyculata	Regression	2.38	8	0.519	0.054
L. groenlandicum	One -Way ANOVA	3.55	5, 11		0.037
L. groenlandicum	Regression	43.104	10	0.497	0.010
V. myrtilloides	One-Way ANOVA	2.42	5,10		0.11
V. myrtilloides	Regression	3.355	8	0.585	0.010

Table 4: Summary of statistical analysis for plant height

Species	**T-stat**	**df**	**R2**	**P-value**
Chamaedaphne	4.09	1,10	0.626	.002
Ledum	4.59	1, 10	0.679	.001
Vaccinium	8.044	2, 9	0.536	.046

Table 5: Summary of statistics for number of leaves

Species	**T-stat**	**df**	**R2**	**P-value**
Chamaedaphne	2.80	10	0.441	0.019
Ledum	5.00	10	0.715	0.001
Vaccinium	2.48	9	0.407	0.035

Table 6: Summary of statistics for leaf size

Species	**T-stat**	**df**	**R2**	**P-value**
Chamaedaphne	-1.393	10	0.163	0.194
Ledum	0.669	10	0.043	0.519
Vaccinium	0.473	9	0.024	0.648

Table 7: Summary of statistics for number of branches

Species & Analysis	**T-stat**	**R2**	**P-value**
Chamaedaphne Regression	1.291	0.143	0.226
Ledum Regression	3.294	0.520	0.008
Vaccinium Regression	0.886	0.080	0.399

Table 8: Summary of Statistics for branch length

Species	**T-stat**	**R2**	**P-value**
Chamaedaphne	3.16	0.564	0.036
Ledum	3.06	0.511	0.013
Vaccinium	2.74	0.456	0.023

Table 9: Summary statistics of foliar estimates

Species / Test	**T-stat**	**R2**	**P-value**
Chamaedaphne Regression	2.120	0.333	0.063
Ledum Regression	5.541	.754	<0.005
Vaccinium Regression	4.616	0.436	0.027

Table 10: Summary of woody estimate statistics

Species / Test	**T-stat**	**R2**	**p-value**
Chamaedaphne Regression	1.662	0.235	0.131
Ledum Regression	5.647	0.761	< 0.005
Vaccinium Regression	2.270	0.364	.049

Table 11: Summary of statistics for foliar: woody estimate

Species / Test	**T-stat**	**R2**	**p-value**
Chamaedaphne Regression	0.981	0.097	0.352
Ledum Regression	1.237	0.133	0.245
Vaccinium Regression	-0.271	0.008	0.793

Table 12: Examples or light saturation and maximal photosynthesis values for light curves measured in control plots based on a minimum of 6 leaves per species.

Species	**Vmax (µmol m^{-2} $leaf^{-1}$)**	**Light Saturation (µmol m^{-2} $ground^{-1}$)**
C. calyculata	12.85	700
L. groenlandicum	9.22	700
V. myrtilloides	17.3	1100

Table 13: T-test values for *C. calyculata* and *L. groenlandicum* within control and 20NPK plots. See Figs. 4 and 5 for mean values.

Species/ Test	**T-stat**	**P-value**	**df**
L. groenlandicum Light Response	2.58	0.021	11
C. calyculata Light Response	1.607	4.05	18
C. calyculata CO2 Response	5.30	< 0.005	15

Table 14: Summary of C: N data

Species	**T-stat**	**R2**	**P-value**
Chamadaphne	3.041	0.480	.012
Ledum	4.901	0.707	.001
Vaccinium	.015	.000	.988

Table 15: Summary of litter statistics

Sample	**F**	**P-value**	**df**
% Litter plot (inside collar)	12.9	<0.005	5, 12
% Litter sample (outside collar)	25	< 0.005	5, 12
Litter Mass	4.53	0.0149	5, 12